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The consequences of fishing-induced changes in predator size for predator-prey interactions

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Ecology, Evolution, and Marine Biology

by

Rebecca Lee Selden

Committee in charge:

Professor Steven D. Gaines, Chair

Professor Robert R. Warner

Professor Scott L. Hamilton, Moss Landing Marine Laboratories

Professor Christopher Costello

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The dissertation of Rebecca Lee Selden is approved.

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Robert R. Warner

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Scott L. Hamilton

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Christopher Costello

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Steven D. Gaines, Committee Chair

August 2015

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VITA OF REBECCA LEE SELDEN

September 2015

EDUCATION

2015	PhD in Ecology, Evolution and Marine Biology, University of California, Santa Barbara, September 2015 (expected)
2006	A.B. *summa cum laude* in Biology, Bowdoin College, Brunswick, ME.

PROFESSIONAL APPOINTMENTS

2015 -	**NSF OCE Post-doctoral Fellow,** Rutgers University, Department of Ecology, Evolution and Natural Resources, & Institute of Marine and Coastal Sciences. Advisor: Malin Pinsky (beginning September 2015)
2014	**Instructor of Record:** Introduction to Ecology, Ecology Evolution & Marine Biology UCSB
2012-2013	**Guest Lecturer:** Biology of Fishes, Environmental Process in Oceans and Lakes, Ecology, Evolution and Marine Biology, UCSB
2012, 2009	**Teaching Assistant:** Biology of Fishes, Ecology, Evolution and Marine Biology, UCSB
2010-2011	**CA Sea Grant Trainee:** Effects of Marine Reserves on Behaviorally-mediated Changes in Spawning Success of California Sheephead
2006-2007	**Principal Investigator**, Thomas J. Watson Fellowship "Sea Turtle Conservation: Impacting Human and Turtle Populations" Cayman Islands, South Africa, Australia, Malaysia, Panama

GRANTS IN SUPPORT OF RESEARCH

2013	UCSB Associated Students Coastal Fund ($7360)
2012	Worster Family Award for joint research with UCSB undergraduate ($2850)
2012	UCSB Graduate Division Grant ($3000)
2012	Lerner Gray Fund for Marine Research ($1000)
2009-2012	Luce Environmental Science to Solutions Fellowship ($6000)
2006-2007	Thomas J. Watson Fellowship ($25,000 for stipend and research)

FELLOWSHIPS AND AWARDS

2015-2017	National Science Foundation Ocean Sciences Post-doctoral Research Fellowship, Department of Ecology, Evolution and Natural Resources, Rutgers University
2012-2015	National Science Foundation Graduate Research Fellowship
2010-2012	National Defense Science and Engineering Graduate Fellowship
2008	EEMB Graduate Fellowship Award, UC Santa Barbara

PUBLICATIONS

Selden, RL, Valencia, SR, Larsen, AE, Cornejo-Donoso, J, Wasserman A. (2015) Evaluating seafood eco-labeling as a mechanism for ecosystem-based fisheries management. *In revision.*

Boada, J, Sanmartí, N, **Selden, RL,** Lucas, A, Pérez, M, Alcoverro, T, Romero, J (2015) Evaluating potential artifacts of tethering techniques to estimate predation on sea urchins.

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Nicolás L. Gutiérrez, Sarah R. Valencia, Trevor A. Branch, David J. Agnew, Julia K. Baum, Patricia L. Bianchi, Jorge Cornejo-Donoso, Christopher Costello, Omar Defeo, Timothy E. Essington, Ray Hilborn, Daniel D. Hoggarth, Ashley E. Larsen, Chris Ninnes, Keith Sainsbury, **Rebecca L. Selden**, Seeta Sistla, Anthony D.M. Smith, Amanda Stern-Pirlot, Sarah J. Teck, James T. Thorson, Nicholas E. Williams. (2012) Eco-label conveys reliable information on fisheries health to seafood consumers. *PLoS ONE:* 7(8): e43765.

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SELECTED PRESENTATIONS

2014 Selden, R.L., Gaines, S. and Warner, R. *The consequences of fishing-induced changes in predator size for top-down control of prey populations.* International Council for the Exploration of the Sea (ICES) Annual Science Conference September 15-19, 2014, La Coruña, Spain.

2014 Selden, R.L., Gaines, S. and Warner, R. *Predator-prey interactions altered by fishing-induced decreases in predator body size.* Ecological Society of America, August 10-15, 2014, Sacramento, CA.

2011 Selden. R.L. *Effects of fishing-induced changes in size on sheephead predator-prey interactions.* California Sheephead Research and Management Meeting. Co-organized by the California Department of Fish and Game, and California Sea Grant. University of California, Santa Barbara. Friday April 22, 2011

OUTREACH AND SERVICE

2012-2014 Graduate student representative UCSB Diving Safety Control Board Committee, Small Boating Operations Committee

2012-2014 Developed hands-on experimental learning module examining predator-prey interactions in local rocky intertidal communities for middle school in Oxnard.

2010-2014 Volunteer Judge for Santa Barbara County Science Fair

2010-2011 Coordinator, EEMB Graduate Student Symposium

2009-2011 Member EEMB Graduate Student Advisory Committee

RELATED EXPERIENCE

2015 Bayesian Modeling Short Course, National Socio-Environmental Synthesis Center

2014 Summer Teaching Institute for Associates, University of California Santa Barbara

ABSTRACT

The consequences of fishing-induced changes in predator size for predator-prey interactions

by

Rebecca Lee Selden

Body size has long been recognized as a key driver of species interactions and of an individual's role in the ecosystem. Body size determines the amount, species, and sizes of prey resources an individual can consume, as well as its own susceptibility to predators. Human harvest of predators can result in severe truncations in predator body size that can have cascading consequences on food webs. Where small and large individuals of the same species differ greatly in their diets, as is common in aquatic systems, the absence of large predators may functionally eliminate a key predator-prey linkage.

Recently management agencies have begun to include size-based metrics as targets. As various harvest strategies differentially affect predator size and biomass, the research presented in this dissertation aims to understand the conditions under which truncations in predator size structure will result in additional loss of predator function than would be predicted from predator biomass alone, and where it will therefore be important to maintain predator size distributions. I specifically examine how the type of ontogenetic shift in diet (e.g. prey species or size class), and the shape of the diet switching function (e.g. gradual or abrupt) will affect the consequences of the loss of the largest predators, and the relative utility of various management strategies in maintaining predator function.

In Chapter 1, I examined the tradeoffs between fishery yield and predator function in the ecosystem when preferentially fishing the largest predators. I found that fisheries that

delay harvest until large predator sizes maximize fishery yield but that this virtually eliminates predation on focal prey eaten late in life history when diet shifts are abrupt and occur at or after the size at maturity. In this case, there is a clear tradeoff between fisheries and ecosystem objectives. Instead, where shifts in diet toward late prey are more gradual, targeting the largest predators can achieve a win-win by maximizing yield and achieving predation rates similar to that with other strategies that harvest predators earlier. As such, the optimal fishing strategy to achieve both single-species and ecosystem benefits depends strongly on the interaction between the fishery selectivity pattern and the changes in predator diet with size.

In Chapter 2, I quantified the size-dependence of the predator-prey interaction between herbivorous sea urchins and one of their important predators in southern California kelp forests, California Sheephead. I further examined the consequences of changes in sheephead size and abundance in marine reserves at Catalina Island on size-specific urchin mortality in field predation trials. In my observations of predation of sheephead on urchins, sheephead smaller than 20cm TL do not eat urchins of any size. Thereafter, small sheephead only consumed small urchins, with larger sheephead sizes needed to successfully consume larger urchins, and the largest sheephead preferentially targeted the largest urchins. Inside marine reserves at Catalina, the greater abundance of large sheephead in combination with the observed size-specific capacities for urchin predation led to higher urchin mortality with marine reserve protection, particularly for the largest urchins. Ultimately, by restoring predator size structure, reserves may serve to enhance the resilience of southern California kelp forests.

In Chapter 3, I examined how variation in predator body size distributions and biomass affects the likelihood of size escapes in situations where predators begin eating prey at some threshold size and thereafter consume increasingly larger prey. We focus on California sheephead because of the size dependence of its interaction with herbivorous sea urchins (Chapter 2), and the natural variation in demography where sheephead achieve smaller maximum sizes but higher biomass in the south of its range. We evaluate the consequences of smaller predator body size on top-down control of urchin populations in two scenarios: 1) when overall predator abundance is the same as the population with larger body size, and 2) when predator biomass is the same. With the same numbers of predators, top-down control was significantly weakened by the lack of large sheephead. However, when sheephead biomass was maintained, the absence of large sheephead did not lead to greater urchin abundance, despite lower predation rates overall and much lower predation on large urchins. Higher predation rates on the smallest urchin size classes served as a bottleneck that kept total urchin population at similar levels and prevented a size escape for the largest urchins. This suggests that where predators switch prey size classes in the same species, the loss of the largest individuals does not inherently result in weaker top-down control, if biomass is maintained, but effective control is sensitive to prey growth rates.

The results of this research suggest that the ignoring shifts in predator size structure can under-estimate the effects of fishing on predator function, especially when large predators eat different species than their smaller counterparts. High predator biomass can compensate when diet shifts are to different prey size classes of the same species. Concordance between diet shifts and fishery selectivity can help identify where it will be important to consider changes in predator size in addition to biomass.

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I. Tradeoffs between single-species and EBFM objectives given ontogenetic shifts in diet with predator size

Abstract

Given the increasing calls (and even mandates) for ecosystem-based fisheries management, it is important to understand the tradeoffs in achieving improvements in both fisheries and ecosystem outcomes. Several authors have recently argued that delaying harvest on predators to large sizes is a way to improve both single-species fisheries outcomes and ecosystem objectives. Because this approach concentrates all harvest on the largest individuals, and will result in greater disruptions in predator body size distributions, I examined how variation in the degree of ontogenetic shifts in diet with size will affect the utility of this harvest strategy in maintaining predator function. I found that fisheries that delay harvest until large predator sizes maximize fishery yield but that this virtually eliminates predation on focal prey eaten late in life history when diet shifts are abrupt and occur at or after the size at maturity. In this case, there is a clear tradeoff between fisheries and ecosystem objectives. Instead, where shifts in diet toward late prey are more gradual, targeting the largest predators can achieve a win-win by maximizing yield and achieving predation rates similar to that with other strategies that harvest predators earlier. As such, the optimal fishing strategy to achieve both single-species and ecosystem benefits depends strongly on the interaction between the fishery selectivity pattern and the changes in predator diet with size.

A. Introduction

In recent years there has been an increasing recognition of the wider ecosystem effects of fishing (Mangel and Levin 2005), with numerous examples of overfishing causing dramatic community reorganization, trophic cascades, and regime shifts (Jackson et al. 2001) in both temperate (Daskalov 2002, Ling et al. 2009, Llope et al. 2011) and tropical (Hughes et al. 2007) systems. These impacts have prompted repeated calls to improve fisheries management, and ecosystem-based fisheries management (EBFM) is one approach that is receiving great interest (Link et al. 2011). EBFM is a more holistic management approach that aims to sustain ecosystems and the fisheries they support by accounting for the interrelationships between fisheries and other ecosystem components (Pikitch et al. 2004).

Despite increasing calls for EBFM by many scientists and mandates by some management agencies and governments, implementation of EBFM has been hindered by a lack of operational objectives and reference points (Brodziak and Link 2002) and a perception that complicated models are needed to adequately take ecosystem dynamics into account. Some critics have questioned the capacity of management agencies to effectively institute more complicated systems of management if comparatively simple single-species approaches are being inadequately implemented (Valdimarsson and Metzner 2005), fueling interest in the development of simple ecosystem-based indicators.

In one widely utilized single-species management approach, yield per recruit is assessed as a function of the fishing effort and the age or size at first capture. Fisheries scientists have understood for decades the benefits to yield of delaying harvesting until the age at which the additional gains that could be achieved by waiting for fish to grow

another year is balanced by losses due to mortality (Beverton and Holt 1957). Based on this approach, the optimum age to harvest occurs when cohort biomass, or the product of weight at age and numbers at age, is maximized in the absence of fishing. As a result, optimal fishery selectivity, or the relative probability of fish being captured by the fishing gear as a function of the age or size of the fish, would have a value of one above this optimal age of harvest and zero below it. This age has been coined A_{opt}, and L_{opt} is the length corresponding to this age (*sensu* Beverton 1992); Figure 1). Froese et al. (2008) recently proposed that there were ecosystem-level benefits derived from harvesting fish at or above this size. The authors made the case for delaying harvest until L_{opt}, using an analysis of 9 fish stocks from the North Sea and the Baltic. Considerable gains in both yield and stock biomass could be achieved by harvesting at L_{opt} relative to the current harvesting regime, which harvests at much smaller sizes. They argue that harvesting at L_{opt} may have a smaller impact on stocks and therefore could contribute to the goals of ecosystem-based fisheries management, by allowing fished predators to fulfill their ecological roles.

Although an L_{opt} strategy does leave small predator individuals relatively untouched and can result in greater predator biomass, it concentrates harvest on the largest individuals. In fact, the theoretical maximum yield per recruit is achieved if all fish greater than L_{opt} are captured (i.e. an infinite fishing mortality at this size; Beverton 1992). As a result of this type of harvesting strategy, the predator size distribution is skewed toward small individuals. Because of their greater energetic requirements, large predators consume more prey per capita than small predators. If small and large predators consume the same prey species, small predators may be able to compensate for the loss of

large individuals. However, in aquatic systems, where predators often grow through four orders of magnitude in size throughout their lifetimes, it is common for diets to change substantially as predators grow (Werner and Gilliam 1984). Recent empirical estimates from eight ecological food webs suggest that the average diet overlap between adjacent size classes of predatory species without metamorphosis was only 40% (Rudolf and Lafferty 2011). The prey items chosen by fish predators are often related to their gape size, resulting in substantial ontogenetic shifts as they grow. Most species of piscivorous fish begin life feeding on zooplankton, shifting to benthic macro-invertebrates before finally extending their diets to fish prey (de Roos and Persson 2013). Likewise many predators that specialize on hard-shelled prey like molluscs and urchins as adults, such as fish in the family Labridae, shift from soft-bodied prey at a body size at which their jaws achieve a certain crushing strength (Wainwright 1991). Where such ontogenetic shifts in diet are relatively discrete and occur at or above L_{opt}, selectively harvesting the largest predator individuals may completely eliminate a predator-prey interaction, and release that focal prey species from top-down control. In some instances, substantial increases in this focal prey can trigger ecosystem regime shifts, such as when herbivorous urchins (Ling et al. 2015) or fish (*Siganus* spp. in the Mediterranean; Sala et al. 2011) are released from predation in temperate macroalgal systems. The decline in top-down control may ultimately result in changes to ecosystem function and loss of key ecosystem services. Alternatively, release of prey may be beneficial where this prey is also harvested. In fact, culling predators to benefit fisheries for their prey has been suggested as one way to maximize ecosystem based yield (Yodzis 2001, White et al. 2012). In

either case, ontogenetic shifts in diet will alter the relative benefits and costs of fishing predators for a given fishery selectivity.

Given the increasing calls (and even mandates) for EBFM, it is important to understand the tradeoffs in achieving improvements in both fisheries and ecosystem outcomes. It is often assumed that conservation objectives come at the cost of fisheries production (Lester et al. 2012). If changing the fishing regime to harvesting at L_{opt} could indeed achieve win-win outcomes in both single-species and ecosystem-based management scenarios, the approach would be appealing, because it provides a simple rule that could be applied to the many data-poor fisheries that make up more than 80% of the global fisheries catch (Costello et al. 2012). However, making the switch would likely require modifications to current fishing gear and practices that could incur significant initial costs to fishermen. Understanding the conditions under which the tradeoffs in yield and ecosystem benefit are most intense will help to identify the fisheries and ecosystems where this strategy may be most cost-effective.

In this paper, we evaluate whether harvesting at L_{opt} can be used as a simple harvest rule to achieve improvements in both single species and ecosystem outcomes when predator diets differ as a function of predator size. We compare the effect of different patterns of size-specific fishery selectivity on the predator size distribution, as well as on a metric of ecosystem impact and predator function (estimated as the degree of reduction in predation by the predator population when harvested relative to an unfished state). We examine the tradeoff between fisheries yield and prey consumption by the predator population based on different fishery selectivity patterns, given variation in predator demographic parameters and changes in diet with predator size.

We begin by examining the effects of different fishery selectivity patterns on a generic predator with life history characteristics representative of those in the cod and haddock family (Gadidae). We use a population dynamics model for the predator to simulate prey consumption by an unfished predator population and then simulate fisheries yield and prey consumption under four selectivity regimes. We examine the effect of fishing on total prey consumption as well as consumption of focal prey eaten at different points in the life history. We then use two case studies to evaluate the tradeoffs in yield and predation: Atlantic Cod (*Gadus morhua)* in the North Sea, and Pacific Cod (*Gadus macrocephalus*) in the Gulf of Alaska. Both cod are important predators in their respective ecosystems, and both undergo ontogenetic shifts in diet. We examine the relative reduction in predation on prey eaten early and late in the life history as a function of fishery selectivity.

B. Methods

1. Population dynamics model with varying fishery selectivity

We constructed deterministic age-structured population dynamics models to examine the consequences of fishery selectivity and life history traits on predation by both a generic gadid predator and for two case studies with Atlantic Cod and Pacific Cod. In this model, size-specific mortality is the sum of natural mortality and the product of fishing mortality and selectivity. In this way, we can independently vary the relative intensity of harvest as well as the relative probability of capture as a function of age that together affect total predator biomass and the biomass distribution across predator sizes. We utilized a standard fisheries age- and size-structured population dynamics model

(Cope and Punt 2009). The equations describing the model, the parameter values used, and sensitivity analyses are provided in the supplementary methods (Appendix).

2. Fishing dynamics

We evaluated the effect of fishing with three selectivity patterns. The first approach followed Froese et al. (2008), by delaying harvest until L_{opt}, which is defined by the natural mortality rate (M), the von Bertalanffy growth coefficient (k) and asymptotic size (L_∞) from the von Bertalanffy growth equation describing length at age (L_A): $L_A = L_\infty(1 - exp(-kA)$, and the length-weight scaling exponent (b in $W_A = aL_A^b$, where W_A is the weight at age; Froese et al. 2008, Hordyk et al. 2015), such that:

$$L_{opt} = L_\infty \frac{b}{\frac{M}{K}+b}. \quad (1)$$

However, determining L_{opt} depends on accurate representations of natural mortality, and this parameter is notoriously difficult to estimate. Historically, in the absence of information a value of 0.2 has often been assumed for natural mortality, or more recently calculated from empirical relationships between natural mortality and other more easily estimated life history parameters. On the other hand, data on age or length at maturity is readily available or relatively easily acquired. Many current size limits are based on the size at maturity, driven by the concept of allowing fish to spawn at least once before harvesting. Thus, the second approach compared the performance of selectivity patterns following the maturity ogive, or the proportion of fish mature in each age class, [hereafter "Maturity"] to that in which only fish > L_{opt} are harvested [hereafter "L_{opt}"]. Thirdly, we considered one additional selectivity pattern that violated the simple

rules proposed by Froese (2004) to avoid overfishing: a non-selective fishery beginning at age 0 [hereafter "non"].

Values for F (mortality due to fishing) ranged from 0 (unfished) to 3. The F-values corresponding to maximum sustainable yield (F_{MSY}) and those that reduced the population to 40% (F_{40}) of the unfished spawning biomass per recruit were also calculated, since these are reference points frequently used in management. Relative catch was defined as the yield relative to that resulting from the L_{opt} strategy.

3. Effects of fishing on predation

We used the resulting abundance and size distribution of the predator population simulated by the population dynamics model to estimate annual prey consumption by the predator population. Daily food consumption per unit biomass (C_A) was defined from weight at age, and parameters from the von Bertalanffy growth curve (Essington et al. 2001):

$$C_A = \frac{(H/E){W_A}^{d-1}}{365}, \quad (2)$$

where d is the allometric slope of consumption (assumed to be 2/3 with von Bertalanffy growth), E = assimilation efficiency, assumed to be 0.65 (Holsman and Aydin 2015), and $H = 3K{W_\infty}^{1-d}$, represents the assimilation constant, with W_∞= the weight at the maximum length.

Annual prey consumption by the predator population was calculated as

$$365 \sum_A^\omega N_A W_A C_A \theta_{A,i}, \quad (3)$$

where $\theta_{A,i}$ is the percentage of the diet of a predator of age A comprised of prey i. For total prey consumption, $\theta_{A,i} = 1$. We also considered predation on prey eaten

differentially throughout the life history of the predator: (1) prey eaten early then shifting abruptly away from the prey at $0.5L_{\infty}$, and (2) prey only eaten late in the life history when the predator has reached L_{opt}. We define relative predation as the prey consumption relative to an unfished predator population. We examined relative predation as a function of the range of F values, as well as at F_{MSY} and F_{40}.

4. Case Studies

a) North Sea Cod:

One of the species highlighted in Froese et al. (2008) was North Sea Atlantic Cod (*Gadus morhua)*. The current selectivity regime begins harvesting cod even before the size at maturity (Fig. A1), and substantially earlier than L_{opt}. As a result, Froese et al. (2008) found considerable gains in both yield and stock biomass were achieved by harvesting at L_{opt} relative to the current harvesting regime. However, cod, like many piscivores, exhibit an ontogenetic change in diet with size, with an increasing proportion of the diet comprised of fish as they grow (Van Leeuwen et al. 2008). Reductions in piscivory by cod due to overfishing in the Baltic Sea are thought to have contributed to the release of their clupeid prey, which then inhibited subsequent cod recovery due to competition with larval cod, predation on cod eggs, and/or decreased production of the size classes of prey needed for juvenile cod because of increased density-dependence in the prey (Gårdmark et al. 2015). This is thought to have led not only to a phase shift, but also an alternative stable state characterized by clupeid dominance. Given the increased piscivory by larger size cod, we evaluated the effect of different selectivity regimes on piscivory by cod populations.

We compared outcomes for single species and ecosystem metrics for the following scenarios: (1) current selectivity and current F [hereafter "current"]; (2) current selectivity at F_{MSY} [hereafter "ICES-MSY"]; (3) L_{opt} selectivity with F that achieves the same yield as the MSY for the current selectivity [hereafter "L_{opt} Equal"]; (4) L_{opt} selectivity at F_{MSY} [hereafter "L_{opt} MSY"]; (5) L_{opt} selectivity at current F [hereafter "L_{opt} current"].

Ontogenetic shifts in diet with size were estimated for North Sea Atlantic Cod using the DAPSTOM diet database (Pinnegar 2014; N = 152,522 stomachs). Prey weights were unavailable for the majority of the stomach records. As a result, diet composition was determined from the fraction of the total number of stomachs containing a particular prey item (i.e. the frequency of occurrence). The frequency of occurrence of each prey group was calculated for each 5 cm length bin. The frequency of occurrence for fish and non-fish prey as a function of length bin was estimated using a linear model and used to predict diet composition for each length at age in the population dynamics model (Table A6). The relative effect of the selectivity regime on consumption of fish and non-fish prey was assessed.

b) Gulf of Alaska Pacific Cod:

A climate-induced regime shift in the 1970s in the Gulf of Alaska led to a switch in dominance by decapod crustaceans and small pelagic fish to one dominated by groundfish, including Pacific Cod (Litzow and Ciannelli 2007). Increased predation by Pacific Cod was suggested as a potential cause of the collapse of several crustacean fisheries in the area, including pink shrimp and several crab species (Albers and

Anderson 1985), and the resulting shift in top-down control has been attributed as a driver of community reorganization (Litzow and Ciannelli 2007). Pacific Cod in the Gulf of Alaska display strong changes in diet with size (Urban 2012). At intermediate sizes, Pacific Cod consume crab species upon which several commercial fisheries depend. At large sizes, Pacific Cod switches almost exclusively to prey upon Walleye Pollock *Theragra chalcogramma* (Urban 2012), the target for one of the largest, most valuable fisheries in the world. It is therefore important to understand how different fishing strategies and the resulting changes in Pacific Cod size structure will affect their consumption of commercially important prey, and thereby affect the fishery productivity of Walleye Pollock as well as the recovery potential of the crab fisheries.

Ontogenetic shifts in diet with size were assessed using diet data for Pacific Cod (N = 6,477 predator stomachs) in the Gulf of Alaska 1981-2009 from the Resource Ecology Fish Foods Habits Database (http://www.afsc.noaa.gov/refm/reem/data/Default.htm, *pers.comm.,* Zador, AFSC). Diet composition data were pooled across 5 cm length bins. Percent of the diet by weight in each length bin comprised of Walleye Pollock was fit to a logistic function:

$$\theta_{L,pollock} = \{1 + \exp[-\gamma(L - L50_{pollock})]\}^{-1}, \quad (4)$$

where $L50_{pollock}$ is the size at which 50% of the diet is comprised of pollock, γ is the slope of diet fraction at $L50_{pollock}$. Percent of the diet by weight comprised of crab was fit to a normal curve:

$$\theta_{L,crab} = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{1}{2}\left(\frac{L - L_{target}}{\sigma}\right)^2\right), \quad (5)$$

where L_{target} is the target length at which the diet fraction is at a maximum, and σ is the width of the diet fraction. Parameter values were fit by minimizing the residual sum

of the squared error between observed and predicted values (Table A6). Predator length bins with fewer than 20 stomachs were excluded from the fitting procedure.

While both predators undergo ontogenetic shifts in diet, the optimal level of predation from a manager's perspective likely differs for the two predators. With Atlantic Cod, increasing predation on clupeids could be of benefit in that it would make it less likely for high clupeid abundance to adversely affect cod populations (Gårdmark et al. 2015), and the fishery for clupeids is of lower value (in terms of price per kg) relative to that of cod (FAO 2014). In contrast, strategies that reduced predation by Pacific Cod to the greatest extent may be beneficial because their prey support important fisheries of similar value per unit weight in the case of pollock or of even higher value in the case of Tanner crab (*pers. comm.,* National Marine Fisheries Service, Fisheries Statistics Division. [2015 July 29]).

C. Results

1. General Model

The different selectivity patterns resulted in more than 2-fold differences in yield. The highest yield was achieved by delaying harvest until L_{opt} (Table 1). Delaying harvest until the length at 50% maturity resulted in almost equivalent yields, because the length at maturity is 90% of L_{opt}. With earlier maturity at 65% of L_{opt}, yield was reduced to 80% of that achieved with L_{opt} (Fig. B1). Yield with the L_{opt} fishery was double that of the non-selective fishery.

Despite strong differences in yield, predator biomass was reduced to similar levels (34-36% of unfished levels; Table 1). However, the distribution of this biomass across

sizes was very different between the fishery selectivity strategies (Fig. 2A). The non-selective fishery began harvesting earlier, but used a lower fishing mortality rate in order to achieve its maximum sustainable yield (MSY). As a result, biomass was reduced fairly uniformly across predator sizes, and the size distribution was closer to that of the unfished population (Fig. 2B). In contrast, the late harvest strategies left small predator biomass relatively untouched and intensely harvested the largest individuals, resulting in a much greater deviation from the unfished size structure. Predator numbers were reduced to a much greater extent by the non-selective fishery (Table 1).

The reduction in total predation was qualitatively similar to the reduction in predator biomass (Table A5). For the same yield achieved at MSY for the non-selective fishery, 200% higher predation would be possible by delaying harvest until at least the size at maturity (Fig. 3A). For the same relative effect on predation in the ecosystem, a 180% increase in yield could be achieved by fishing with the L_{opt} or Maturity selection regimes. However, as a result of the differences in predator size structure with the different selectivity patterns, the effects of fishing on focal prey depended on when the prey were eaten in the predator's life history. Predation on prey eaten early in the life history and later dropped from the diet was maintained at much higher levels by delaying harvest until L_{opt} (Fig. 3B), because more small predators were available to consume that prey. In contrast, predation pressure on prey eaten late in the life history was reduced to low levels (10-12% of the unfished level) by delaying harvest to large sizes, and was reduced to a greater extent than with non-selective fisheries (25% of the unfished level; Fig. 3C). This result occurred because the L_{opt} and Maturity selection regimes resulted in

the removal of a large proportion of the predator biomass that was capable of consuming the larger prey species.

2. North Sea Cod

The current harvesting regime for North Sea Atlantic Cod harvests fish earlier than both L_{opt} and L_{mat} (Fig. 4A, Fig. B1), and as a result this strategy is sub-optimal for both single-species and ecosystem outcomes. Total biomass and numbers were reduced to 10% and 46% of unfished levels, and total predation was reduced to 16% of the unfished level (Fig. 4B). Maintaining the current selectivity pattern and harvesting at MSY (ICES-MSY) resulted in a 24% increase in catch and more than a doubling in total predation (Fig. 4B). However, changing the selectivity pattern to harvest fish only at or above L_{opt} would also achieve this improved yield but result in a further doubling in total predation pressure (i.e., 4.5 times the predation of the current harvesting regime). Even greater sustainable yields were possible by increasing the harvest intensity further with the L_{opt} harvest strategy, but this came at the expense of reduced predation pressure on prey populations. Harvesting at the current harvest rate (F=0.57) but delaying harvest until L_{opt} resulted in 1.7 times the current catch with 3.5 times the current predation rate. An additional increase in yield was possible by harvesting at the maximum harvest intensity (F=3), resulting in 3 times the current predation.

The percentage of the diet comprised of fish increased linearly with North Sea Atlantic Cod length (Fig. 4C). Correspondingly, fish predation was reduced to 10% of the unfished level for the current harvesting regime (Fig. 4D). However, in contrast to the results from the general model for discrete shifts in diet composition, the gradual increase

of fish as a proportion of the diet with larger cod sizes did not result in greater reductions in predation when harvesting at L_{opt} relative to the other selectivity patterns for prey. When small predators also eat the focal prey but as a smaller fraction of the diet, a considerable amount of predation is maintained despite the differential removal of large predators above L_{opt}. This is not the case when only the large predators eat the focal prey item. As a result, unless ontogenetic shifts toward a focal prey are abrupt, L_{opt} will be an optimal strategy for both single species and ecosystem outcomes in the North Sea, where it is potentially desirable to maintain piscivory.

3. Pacific Cod

Pacific Cod are currently harvested with a 50% selectivity approximately equal to L_{mat} (Fig. A1). By shifting to a diet almost exclusively derived from pollock after the size at L_{opt} (Fig. 5A and 5B), Pacific Cod demonstrate the type of ontogenetic diet shift shown in the general model to result in greater reductions in predation when harvesting at L_{opt}. If Pacific Cod were managed with a target of MSY with the same stock-recruitment relationship as in the general model, this would result in almost complete elimination of their functional role as pollock predators (Fig. B4). However, the management target is currently estimated as F_{40} by the management agencies, the F that reduces spawning biomass per recruit to 40% of the unfished level. At this reference point, predation on pollock due to the current fishery for Pacific cod is reduced to a greater extent than a hypothetical non-selective fishery, but only by a minor degree (0.30 vs. 0.37 of the unfished level; Fig. 5C). Predation on crab is maintained at 76% of the unfished level compared to 62% of a hypothetical non-selective fishery (Fig. 5D).

D. Discussion

The merits of delaying harvest to maximize yield has been known for decades, and our results confirm that the highest yield was observed with this strategy. Froese et al. (2008) claim that this can also lead to ecosystem benefits, by allowing predators to better fulfill their ecological roles. Because an L_{opt} harvest strategy concentrates all fishing effort on the largest predator individuals, ontogenetic shifts in diet that are commonly observed in marine predators have the potential to compromise the capacity for these predator populations to fulfill that role. Our results suggest that if shifts in diet occur abruptly at or above the age at maturity, predator-prey linkages for prey consumed late in life are virtually eliminated when harvesting optimally at L_{opt} from a single species perspective. However, the effect is greatly reduced if the shift occurs earlier than L_{opt}, or if the change in diet is more gradual.

The consequences of a reduction in predation, and the importance of maintaining predation depend on the degree to which increases in prey biomass represent a desirable outcome (such as when the prey are also fished) or something to be avoided (as in the case of a pest prey, such as sea urchins that overgraze kelp habitat used by other species of commercial and recreational importance (Graham 2004); or where prey compete with or consume small size classes of predators that can cause alternative stable states). The results of this paper suggest that where predator diet changes strongly with size, fisheries that delay harvest until predators reach larger sizes will differentially affect prey eaten late in life history, and therefore the concordance between fishery selectivity and diet composition should be considered when devising optimal harvest strategies. In the case

of pollock, which is one of the most valuable fisheries in the world, harvesting Pacific Cod in a way that would reduce its consumption of pollock may maximize total catch from the system. Given that pollock are eaten almost exclusively by large Pacific Cod size classes, it would be optimal to use a late selective fishery, similar to what is currently employed, in order to reduce consumption of pollock to the greatest extent. In contrast, without taking into account how fishery selectivity patterns interact with ontogenetic shifts in diet, managers of the crab fisheries in the Gulf of Alaska may over-estimate the degree to which fisheries for cod would reduce crab predation, and thus contribute to recovery of these crustacean fisheries.

On the other hand, the population release of clupeid prey due to overfishing Atlantic Cod has been shown to have had detrimental effects on cod population dynamics (Gårdmark et al. 2015), by directly consuming cod larvae or by competing with young cod for food. Because cod begin eating fish fairly early and the proportion of the diet comprised of fish increases only gradually, increasing the size limits to L_{opt} for Atlantic Cod would have diminished rather than exacerbated the negative feedback this produced on cod dynamics. This is because consumption of fish by cod is actually maintained at higher levels than the current fishing regime, even if it were managed properly to achieve MSY.

For predators for which harvesting at L_{opt} creates release in undesirable prey species eaten late in life history, alternative harvest strategies may minimize this effect. Recently, “balanced harvest”, in which harvesting is most intense on small individuals and declines as fish grow larger, has been proposed as an alternative harvest strategy. This may minimize effects on the ecosystem (Garcia et al. 2012), because it has been

shown to cause less deviation from the unfished community size structure (Law et al. 2012).

There may be additional drawbacks of harvesting at L_{opt}. First, fisheries that selectively harvest the largest individuals can lead to evolutionary changes in predator populations in which growth and life history characteristic are altered. Over many generations, these may result in declines in yield (Conover and Munch 2002). Second, achieving the high yields predicted from these models by harvesting at L_{opt} requires intensive harvest rates. Because fishing costs typically increase as the density of the targeted size classes decline, achieving high yields through intensive harvesting often reduces fishery profit (White et al. 2008). If that is the case, the tradeoff curves shown here indicate that the L_{opt} strategy still achieves improved ecosystem outcomes at no cost to yield, and achieving that yield actually occurs at a lower fishing intensity, which would enhance fisheries profit. For Atlantic cod, applying the same harvest intensity as currently employed (F = 0.57), but delaying harvest until L_{opt} resulted in close to a doubling in yield, and improvements in all ecosystem objectives measured here. In addition, if a higher price per kilogram is paid in the market for larger fish, as is the case for cod in Sweden (Cardinale and Hjelm 2012), Iceland (Smith and Gopalakrishnan 2010), and Norway (Zimmermann and Heino 2013), higher profits may still be possible even if fishing costs do increase. A formal quantitative analysis of fisheries costs and net profits is beyond the scope of this paper, but warrants further examination.

E. Conclusions

The optimal fishing strategy to achieve both single-species and ecosystem benefits depends strongly on the interaction between the fishery selectivity pattern and the changes in predator diet with size. In many cases, where harvesting is occurring too early for single-species objectives, win-win outcomes can be achieved by increasing the size limit. Predation is maintained at the highest levels by delaying harvest until at least the size at maturity, except in the cases where diet shifts toward a focal prey also occur at this size. If this focal prey is also targeted by fisheries, total yield from both predator and prey fisheries will be maximized by fishing at L_{opt}. If this focal prey is a pest, in which prey release represents an undesirable outcome, alternative harvest strategies (such as a balanced harvest) may be employed in order to maintain large predator size classes and maintain top-down regulation on prey.

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G. Tables

Table 1. Metrics of fisheries yield, predator stock status and ecosystem outcomes based on fishing with the different selectivity patterns at F_{MSY}. Catch is relative to the maximum possible with L_{opt} selectivity. Predator biomass, predator numbers, and predation levels are relative to an unfished predator population. Total predation is the total prey biomass consumed by the predator population. Early prey is prey eaten early in life history and dropped from the diet after $0.5L_{\infty}$. Late prey are not eaten until after L_{opt}.

Metric:	*Fisheries Yield*	*Predator Stock*		*Ecosystem Outcomes*		
Selectivity	**Relative Catch**	**Relative Biomass**	**Relative Numbers**	**Total Predation**	**Early Prey**	**Late Prey**
L_{opt}	1	0.36	0.77	0.47	0.93	0.10
Maturity	0.94	0.34	0.75	0.45	0.93	0.12
Non	0.52	0.34	0.63	0.40	0.69	0.25

H. Figures

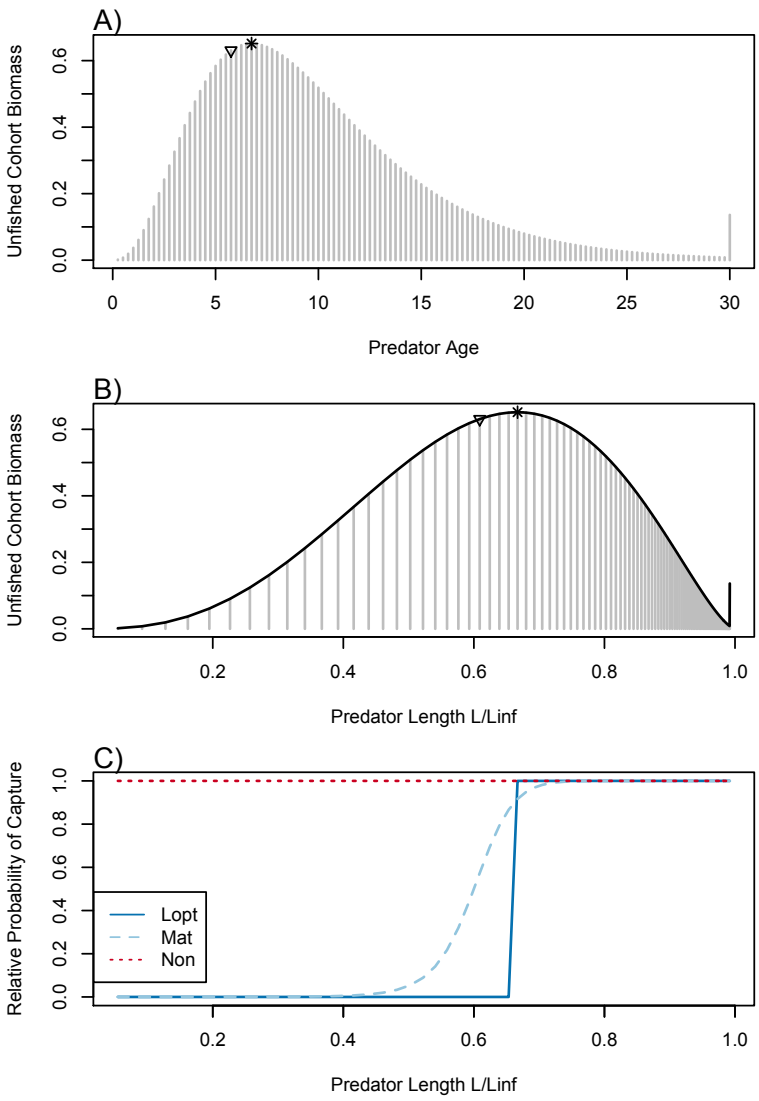

Figure 1. A) Cohort biomass as a function of predator age. The height of each bar represents the product of numbers at age and weight at age. Cohort biomass is maximized at A_{opt}=6.75 years (star), B) Cohort biomass as a function of the ratio of the predator length to the maximum length (L_{inf}). L_{opt} = 0.67L_{inf} (star), and L_{mat}= 0.9L_{opt} (triangle), the median found in Prince et al. (2014). The black line in (B) integrates cohort biomass over all lengths, and will be used in subsequent figures representing cohort biomass. The peak in biomass at age 30 and L_{inf} in the unfished population is due to the inclusion of a plus-group in which all fish that would survive to another year are accumulated in this group. C) Selectivity patterns considered for model. Late selectivity: L_{opt} = only harvest at or above L_{opt}; Mat = harvest intensity is proportional to the maturity ogive, with 50% selectivity at L_{mat}, Early selectivity: Non = a non-selective fishery with full selectivity from earliest age.

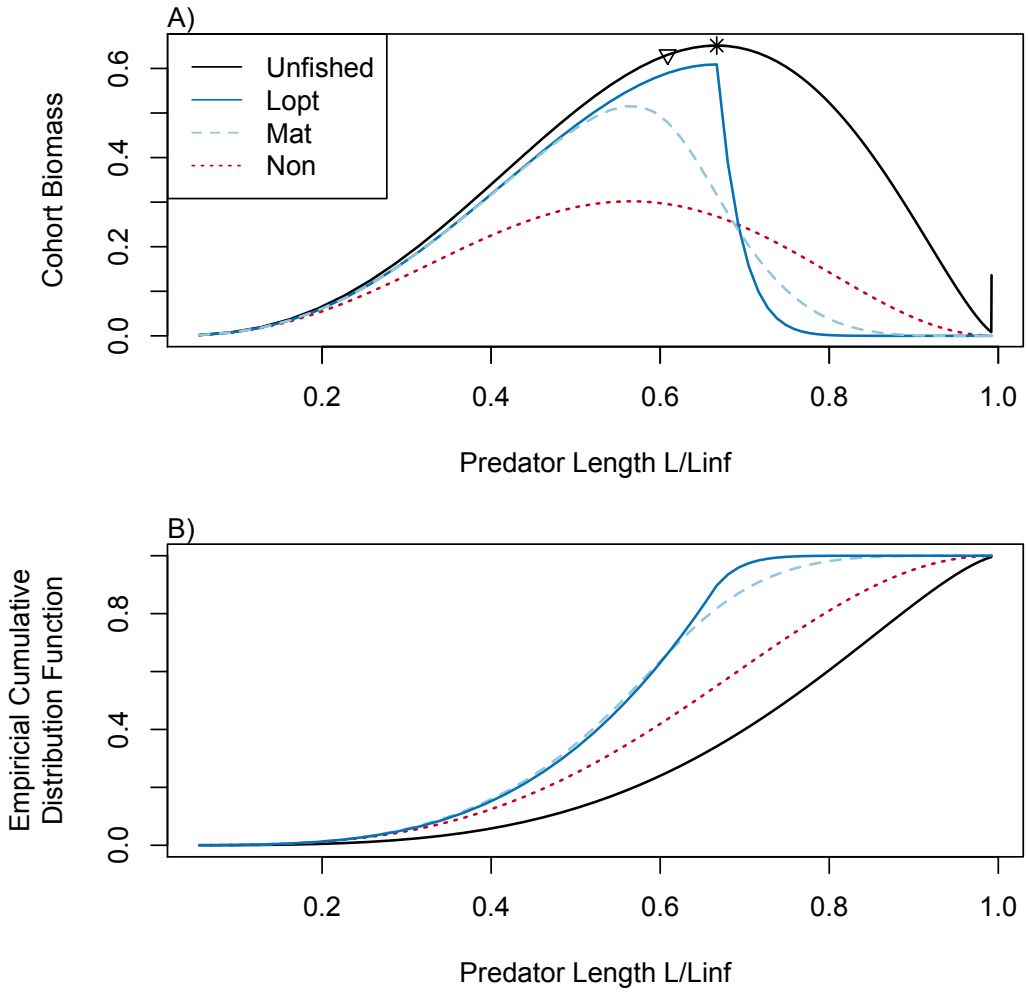

Figure 2. A) Cohort Biomass for the unfished population and when harvesting fish at MSY with each selectivity pattern B) Cumulative distribution function for the size distribution in terms of biomass for the unfished population and the three selectivity patterns.

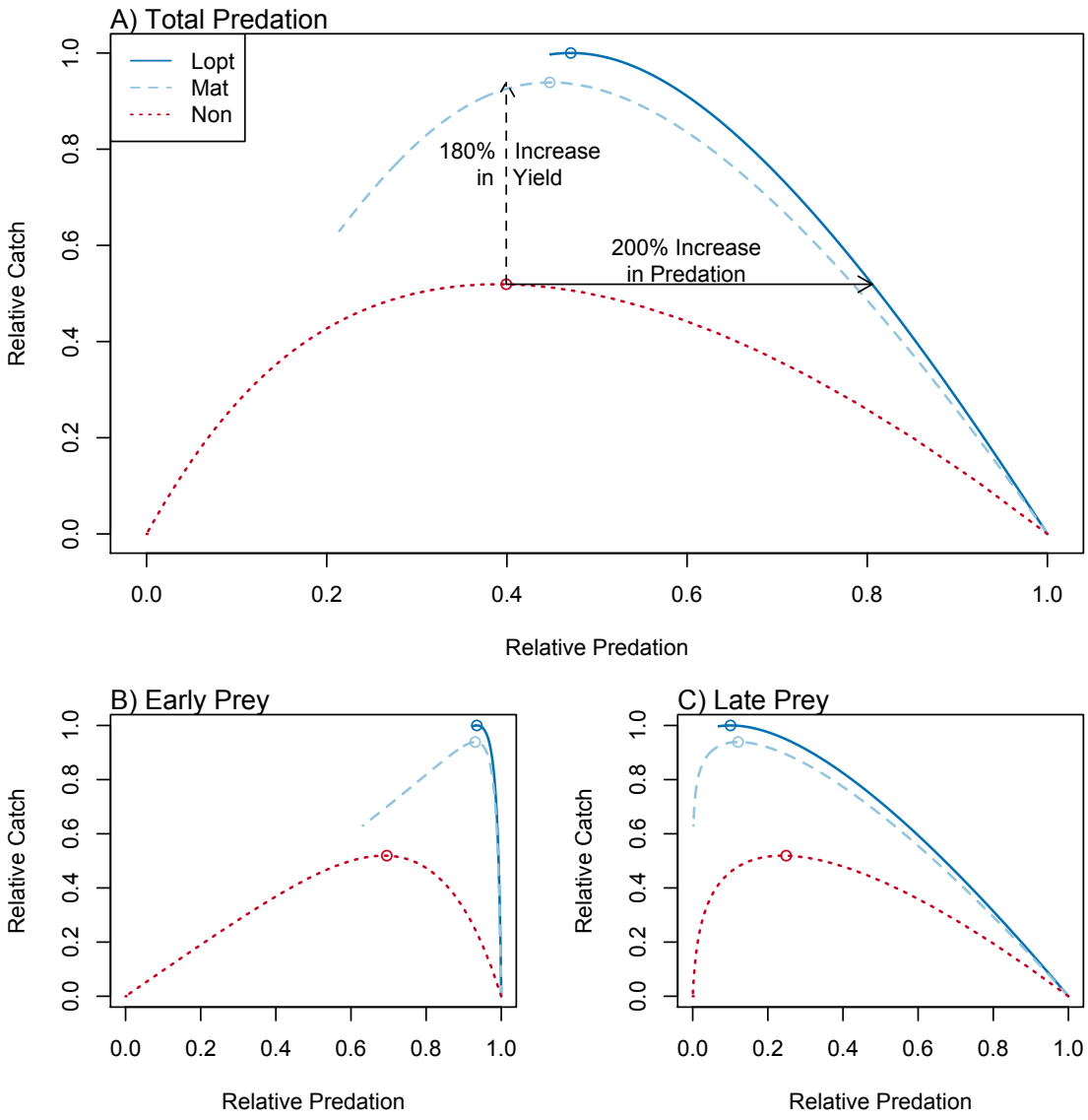

Figure 3. The tradeoff between relative catch (the catch relative to the maximum catch possible with L_{opt} selectivity) and relative predation (the predation with fishing relative to that of an unfished predator population) among fishery selectivity scenarios (L_{opt} = solid dark blue line; Mat = light blue dashed line; Non = red dotted line). The unfished predator population is in the bottom right corner of each graph with a relative predation value = 1, and relative catch = 0. As fishing intensity increases with each fishery selectivity pattern, predation declines and catch initially increases. Tradeoffs represented for A) total predation, B) Early prey: switching away from focal prey at $0.5L_{inf}$, C) Late prey: shift to focal prey at L_{opt}. Open circles represent F_{MSY}. The black solid arrow in A) shows fishing with either the L_{mat} or L_{opt} strategy would achieve 200% higher predation for the same yield as the "non"-selective fishery. The dashed black arrow in A) shows that fishing with the L_{mat} strategy would achieve 180% of the yield as the "non"-selective fishery, for the same amount of predation

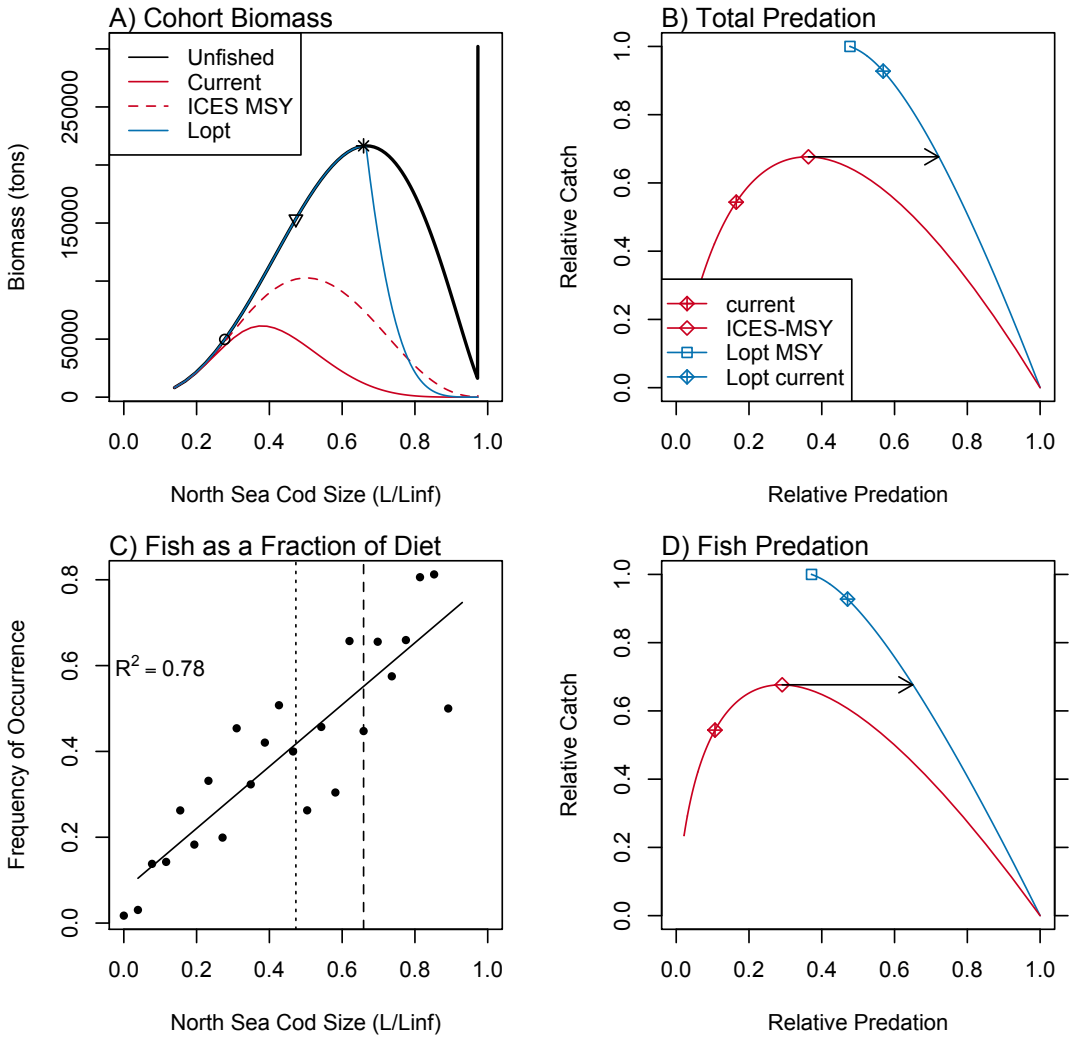

Figure 4. A) Cohort Biomass for North Sea Cod as a function of the different fishing regimes. Star represents L_{opt}; the triangle represents the size at 50% maturity, and the circle represents the current legal size limit of 35cm. Shown are the reductions in cohort biomass due to the current fishing regime which has a 50% selectivity at 38 cm (0.27L/Linf; red lines), at the current fishing rate (F = 0.58; solid line), and at the F_{MSY} (F = 0.21; dashed line). The dark blue line represents the cohort biomass when delaying harvest to L_{opt}, and fishing at the current fishing rate (F=0.58). B) Relative catch vs. relative total predation for the current fishing regime which has 50% selectivity at 38cm (red), and that which only harvests fish at or above L_{opt} (dark blue), Symbols represent values for current fishing regime (red diamond-cross), MSY for current fishing regime (red diamond), and MSY for L_{opt} (open dark blue square). Also depicted is L_{opt} strategy that would achieve the same yield as the MSY in the current selectivity pattern ("L_{opt} Equal": the intersection of dark blue line and black arrow) and the L_{opt} strategy with the same F as current (dark blue diamond). C) Ontogenetic increase in the proportion of the diet comprised of fish. Dashed line represents L_{opt}, and dotted line represents L_{mat}. D) Relative catch vs. relative fish predation with lines and symbols the same as in 4B.

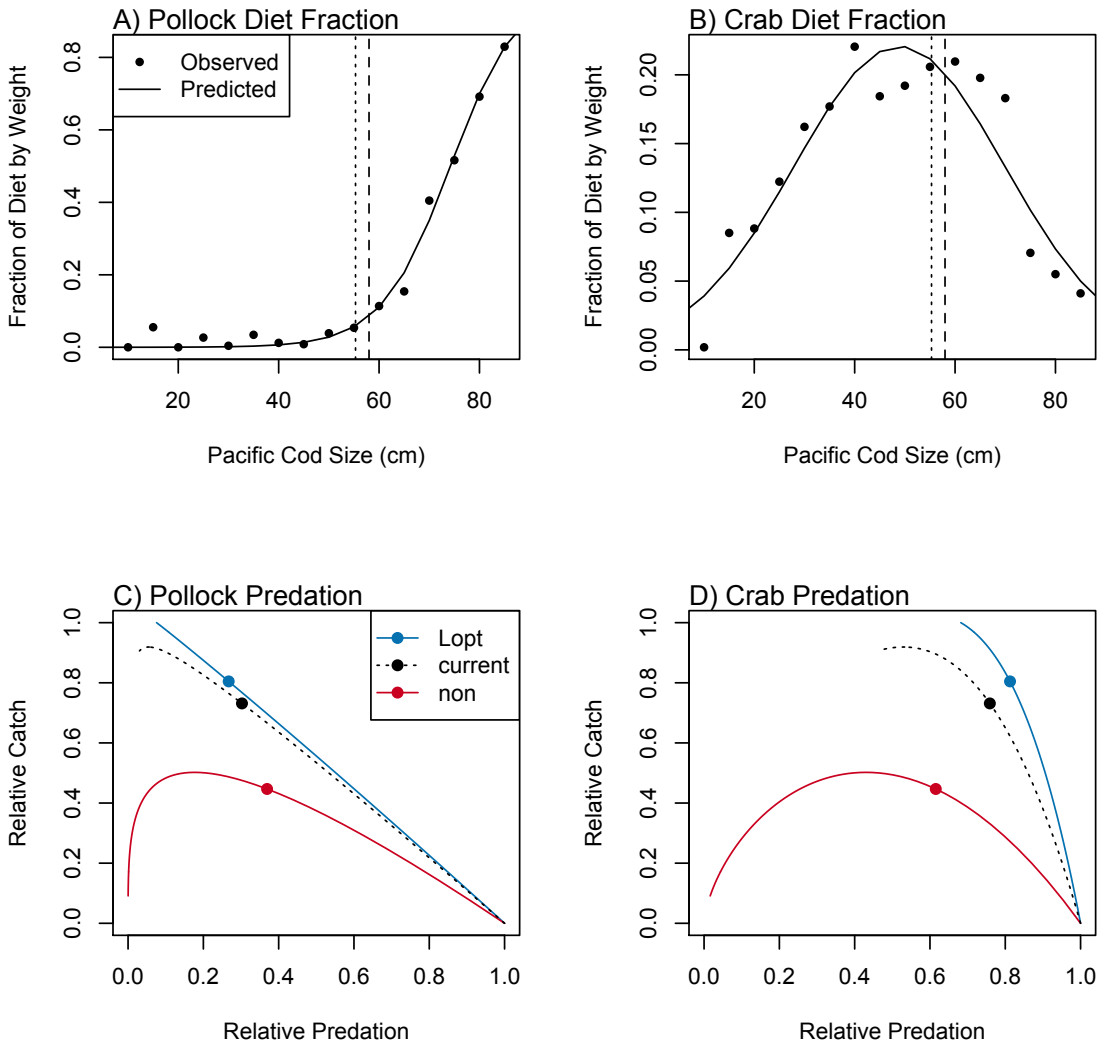

Figure 5. Observed (dots), and predicted (solid line) fraction of diet comprised of A) pollock, and B) crab as a function of Pacific Cod size. Dashed line represents L_{opt}, and dotted line is L_{mat}. Relative catch vs. relative predation for C) pollock and D) crab for the current fishing regime (black dotted line), L_{opt} (blue line), and a hypothetical non-selective fishery (red line). Filled circles represent the values for harvesting at F_{40}.

I. Appendices

Appendix 1.

Details on population dynamics model

The stable age structure for this model with constant recruitment is given by:

$$N_A = \begin{cases} R_F & A = 0 \\ N_{A-1}\exp\left(-(M + FS_{A-1})\right) & 0 < A < \omega \\ N_{A-1}\exp\left(-(M + FS_{A-1})\right)/[1 - \exp\left(-(M + FS_A)\right)] & A = \omega, \end{cases} \quad (1)$$

where N_A is the number of animals of age A, M is the age independent instantaneous rate of natural mortality, F is the fishing mortality when selectivity is equal to 1, S_A is the selectivity of animals of age A in the fishery, ω is the maximum longevity representing a "plus group" in which all fish that would have survived to another year are accumulated in this group, and R_F is the number of recruits based on a modified Beverton-Holt stock-recruit relationship (Cope and Punt 2009) when fishing mortality equals F:

$$R_F = \frac{R_{F=0}[4h\widetilde{S_F} - \widetilde{S_{F=0}}(1-h)]}{\widetilde{S_F}(5h-1)}, \quad (2)$$

where $R_{F=0}$ is recruitment in the absence of fishing, h is the steepness of the stock-recruitment relationship (the fraction of $R_{F=0}$ when spawning biomass is reduced to 20% of the unfished spawning biomass), $\widetilde{S_F}$ is the spawning biomass per recruit when fully selected fishing mortality equals F, and $\widetilde{S_{F=0}}$ is the spawning biomass per recruit in the absence of fishing.

$$\widetilde{S_F} = \sum_{A=1}^{\omega} N_A W_A \delta_A, \quad (3)$$

where δ_A is the fraction of animals of age A that are mature, W_A is the weight of an animal of age A based on the allometric growth model ($W = aL^b$) where length at age is assumed to follow the von Bertalanffy growth function (VBGF):

$$L_A = L_\infty(1 - exp(-k(A - A_0)), \quad (4)$$

where L_∞ is the asymptotic maximum length, k is the growth coefficient, and A_0 is the theoretical age at which fish length would be zero. L_{opt} is defined by the ratio of the natural mortality rate (M), the von Bertalanffy growth coefficient (k), and the length-weight scaling exponent (b) (Hordyk et al. 2015):

$$L_{opt} = L_\infty \frac{b}{\frac{M}{K}+b}. \quad (5)$$

The maturity function is defined as

$$\delta_A = \{1 + \exp[-\log(19)(A - A_{mat})/\beta]\}^{-1}, \quad (6)$$

where A_{mat} is the age at 50% maturity and β is the difference between A_{mat} and the age at 95% maturity (Cope and Punt 2009). β was set to $A_{mat}/4$ as per Cope and Punt (2009). The model was run with an age interval of 0.25 year for greater resolution of lengths. A_{mat} was calculated from L_{mat}, which was based on the median of the empirical relationship between L_{mat} and L_{opt} for the stocks reported in the meta-analysis of Prince et al. (2014).

Yield was calculated using the Baranov catch equation:

$$Y = \sum_{a=1}^{\omega} N_a W_a (1 - \exp(-(M + FS_A)) \frac{FS_A}{M+FS_A} \quad (7)$$

Relative catch was defined as the yield relative to the maximum possible with the L_{opt} strategy.

Life histories and parameter values for gadid predator

The base choice for the parameters was chosen to represent a generic predator in the cod and haddock family (Gadidae) (Table 1). Gadidae represent the family with the 4th largest landings globally (FAO FishStatJ) and four of the top ten seafood groups consumed in the UK (Seafood Choices Alliance). The asymptotic size, L_∞, was set to a

value of 100 cm, a common size for several species in the Gadidae family. The von Bertalanffy growth coefficient k was set to 0.16, the mean value for an L_∞= 100 cm from a log-log regression of L_∞ on k for gadids on FishBase (Froese and Pauly 2014). Natural mortality was assumed to follow the Beverton-Holt life history invariant where M/k = 1.5, yielding an M=0.24. Based on these values, a length-weight scaling exponent equal to 3, and equation (5), L_{opt}= $0.67L_\infty$. While the results were developed for a predator with a maximum size of 100cm, the baseline results will apply to any fish with an M/k = 1.5, because this ratio, and not their absolute values, determines the distribution of biomass across sizes as a function of length relative to the maximum length in the unfished population (Hordyk et al. 2015). The steepness of the stock recruit relationship was set equal to 0.8, the median value for Gadidae in Myers et al. (1999), and the size at maturity was based on the median value for L_{mat}/L_{opt} in Prince et al. (2014).

Sensitivity analyses

The recent meta-analysis of Prince et al. (2014) showed that the ratio of the natural mortality rate (M) to the von Bertalanffy growth coefficient (k) can differ considerably from the Beverton-Holt life history "invariant" of M/K = 1.5. We explored the effects of different selectivity patterns on single species and ecosystem metrics for predators with M/k = 1 and M/k = 3, where $L_{opt} = 0.75L_\infty$ and $0.5L_\infty$, respectively. We also explored the effect of different assumptions about the steepness of the stock-recruitment relationship (h = 0.65, the 20th percentile for Gadidae in Myers et al. (1999) and h=0.5), and earlier maturity (L_{mat}/L_{opt} = 0.65, the 10th percentile in Prince et al. (2014) and 25th percentile for U.S. west coast groundfish in Cope and Punt (2009)).

Atlantic Cod

Life history parameters for Atlantic Cod were extracted from Froese et al (2008), and the most recent North Sea Cod Stock assessment (ICES 2012) (Table 2). The current selectivity pattern was estimated by fitting F at age from the most recent North Sea Cod stock assessment (ICES 2012) to the following age-based selectivity equation (Thorson and Prager 2011), by minimizing the residual sum of squared errors (SSE: $SSE = \sum_{i=1}^{n}(y_i - \hat{y})^2$) between observed and predicted selectivity using the non-linear optimization algorithm of Microsoft Excel's SOLVER program (Cochrane 2002):

$$S_{A,ICES} = (1 + \exp(-s(A - A50.sel))^{-1} \quad (8)$$

where *A50.sel* is the age at 50% selection, and *s* is the slope at *A50.sel* (Table A5, Figure A1).

We explored the effects of different selectivity regimes on yield, biomass distributions, and predation with a constant natural mortality of M = 0.21 derived from the estimate of the von Bertalanffy growth coefficient and an M/K=1.5 (Froese et al. 2008), reported in the main text, and with the age-dependent natural mortality estimated by the most recent stock assessment for 2010 (ICES 2012; Table A3). Results for the simulations with age-dependent natural mortality are reported in Appendix B.

Pacific Cod

Life history parameters were extracted from the 2013 Gulf of Alaska Pacific Cod stock assessment (A'mar and Palsson 2013; Table A4). The current selectivity was estimated from the effective F at age for 2008-2012 (A'mar and Palsson 2013) as in

equation (8), and the size at 50% selectivity is very close to L_{opt} (Figure A1, Table A5). While the ascending limb of the current selectivity closely matches the logistic selectivity curve, effective fishing mortality from the current fishery declines at older ages. As a result, the mean selectivity for 2008-2012 was used to simulate the current fishing regime (Figure A1). Due to a lack of reliable estimates for MSY, the fishery currently has a target fishing mortality of F_{40}, the fishing rate that reduces spawning biomass per recruit to 40% of the unfished level (A'mar and Palsson 2013). The consequences of fishing for predation using MSY as a target were also explored assuming the same stock-recruitment relationship as that in the general model. Results are reported in Appendix 2.

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Table A1. Parameter values for a gadid predator in baseline scenario.

Parameter	Value	Reference
L_∞	100	FishBase
k	0.16	FishBase
A_0	-0.1	
ω	30	
M	0.24	Beverton-Holt life history invariant (M/k=1.5)
h	0.8	Myers et al. 1999
a	0.01	FishBase
b	3	FishBase
L_{opt}	$0.67L_\infty$	$b/(b+M/k)$
L_{mat}/L_{opt}	0.9	Prince et al. 2014

Table A2. Parameter values for North Sea Atlantic Cod

Parameter	Value	Reference
L_∞(cm)	129	Froese et al. 2008
k (year $^{-1}$)	0.14	Froese et al. 2008
A_0 (years)	-0.82	Froese et al. 2008
ω	25	ICES FishMap ("ICES FishMap" n.d.)
M	0.21	M/k=1.5, Froese et al. 2008
h	1*	ICES 2012
a	0.01	Froese et al. 2008
b	3	Froese et al. 2008
L_{opt}	86	b/(b+M/k)
$Lmat/L_{opt}$	0.71	
R0 (thousands)	141,266	Froese et al. 2008

*Reference points are assessed by ICES based on average recruitment rates (R0) and per recruit analyses. This implicitly assumes an h=1. $F_{MSY}=F_{max}$.

Table A3. Age-dependent natural mortality for North Sea Atlantic Cod

Age	Age-dependent M
1	1.038
2	0.698
3	0.490
4	0.233
5	0.2
6	0.2
7	0.2

Table A4. Parameter values for Pacific Cod

Parameter	**Value**	**Reference**
L_∞(cm)	101	A'mar and Palsson 2013
k (year^{-1})	0.166	A'mar and Palsson 2013
A_0 (years)	-0.275	A'mar and Palsson 2013
ω	20	A'mar and Palsson 2013
M	0.38	A'mar and Palsson 2013
h	1*	A'mar and Palsson 2013
a	0.0088	A'mar and Palsson 2013
b	3.084	A'mar and Palsson 2013
L_{opt}	58	*b/(b+M/K)*
$Lmat/L_{opt}$	0.95	A'mar and Palsson 2013
R0 (thousands)	239,198	A'mar and Palsson 2013

*The Stock Synthesis model assumes a steepness of 1, and uses F40 as its estimate of FMSY (A'mar and Palsson 2013).

Table A5. Selectivity fitting results for North Sea Cod and Pacific Cod

	North Sea Cod 2000-2011	Pacific Cod 2008-2012
N	84	95
s	1.99	1.79
A50.sel (years)	1.65	4.266
L50.sel (cm)	37.7*	53.2

* 35 cm is the legal landing length

Table A6. Diet fitting results for North Sea Cod and Pacific Cod.

		Value	SE	p	R^2
North Sea Cod					0.78
Fish	Intercept	0.07	0.04	0.08	
	Size	0.0056	0.0006	<0.001	
Pacific Cod					
Pollock	L_{50} γ	74.225 0.1465			
Crab	$L_{.target}$ σ	48.93 20.93			

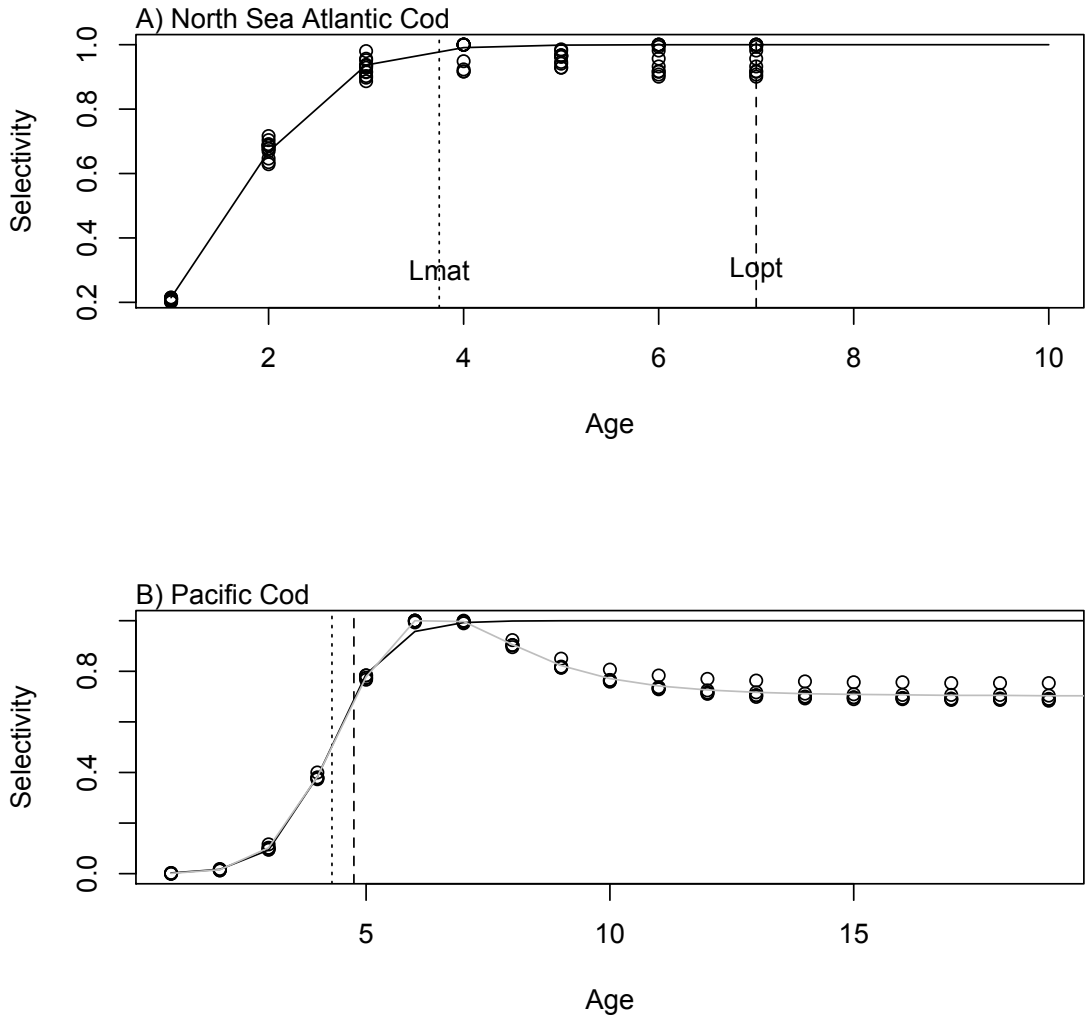

Figure A1. Observed (open circles) and predicted (solid black line) selectivities for A) North Sea Cod (2000-2011), B) Gulf of Alaska Pacific Cod (2008-2012). Dashed line represents L_{opt}, and the dotted line represents L_{mat}. In B) the solid gray line is the mean selectivity estimated from the effective F for 2008-2012, which was used in the simulation of the current fishing regime.

Appendix 2: Supplementary Results

Predation at F_{40}

When harvesting at a level that achieves 40% of the spawning biomass per recruit, instead of MSY, similar qualitative patterns were found between selectivity patterns but with lower values for yield, higher predator biomass and numbers and higher levels of predation (Table B1).

Sensitivity to variation in life history parameters

For a predator with a higher rate of natural mortality, optimal fishing intensity with L_{opt} from a single-species perspective was higher, because fewer fish would survive to another year due to the higher rates of natural mortality. As a result, fishing at L_{opt} at MSY resulted in a more severe reduction in predation for late prey relative to M/K = 1.5 (Fig B1). With a lower ratio of natural mortality to growth of M/K = 1, the converse was true.

With a lower steepness value for the stock-recruitment relationship, and therefore a stronger dependence of recruitment on stock biomass, it is optimal from a single-species perspective to maintain higher predator biomass. As a result, predation on late prey was less severely reduced by fishing with late selectivity (Fig. B2). Earlier maturation did not significantly alter the levels of predation at MSY for any prey, but predation on late prey at F_{40} with an L_{opt} selectivity was lower than with the baseline (Fig B1), because 40% of virgin spawning biomass per recruit was possible with greater depletion of the largest predator individuals.

Atlantic Cod with age-dependent natural mortality

Using age-dependent natural mortality rather than a constant natural mortality rate had no effects on the qualitative pattern of the results (Figure B3), or the relative effect of the fisheries selectivity on fish consumption.

Pacific Cod harvested at MSY with steepness = 0.8

If Pacific Cod were harvested at MSY assuming the same steepness of the stock-recruitment relationship as for the generic gadid, the current fishery and the fishery which delayed harvest to L_{opt} would result in an almost complete elimination of Pacific cod as predator of pollock (Figure B4).

Table B1. Metrics of fisheries yield, predator stock status and ecosystem outcomes based on fishing with the different selectivity patterns at F_{40}. Catch is relative to the maximum possible with L_{opt} selectivity. Predator biomass, predator numbers, and predation levels are relative to an unfished predator population. Total predation is the total prey biomass consumed by the predator population. Early prey is prey eaten early in life history and dropped from the diet after $0.5L_{\infty}$. Late prey are not eaten until after L_{opt}.

Metric:	*Fisheries Yield*	*Predator Stock*		*Ecosystem Outcomes*		
Selectivity	**Relative Catch**	**Relative Biomass**	**Relative Numbers**	**Total Predation**	**Early Prey**	**Late Prey**
L_{opt}	0.87	0.53	0.86	0.63	0.97	0.35
Maturity	0.81	0.52	0.85	0.62	0.97	0.36
Non	0.47	0.50	0.74	0.55	0.80	0.42

Supplementary Figures

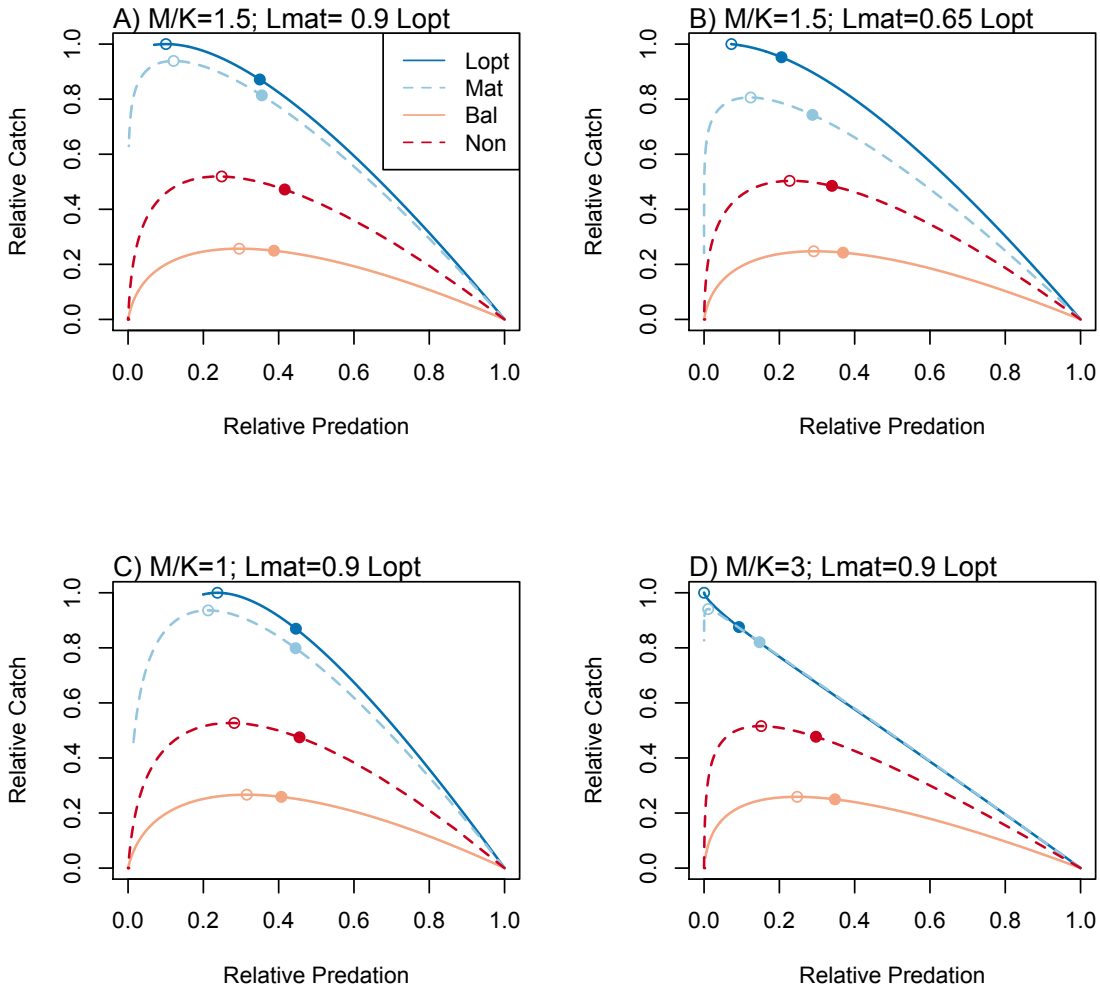

Fig B1. Sensitivity of predation on prey eaten after L_{opt} to changes in the size at maturity, and the ratio of natural mortality to the von Bertlanffy growth coefficient. A) Baseline used in main text; B) earlier maturation; C) lower rate of natural mortality; D) higher rate of natural mortality.

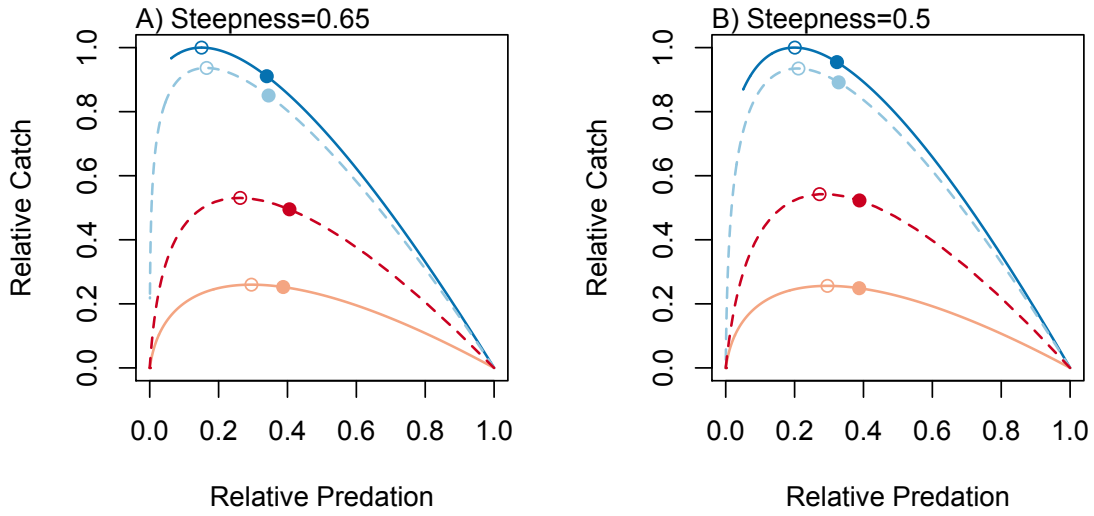

Fig B2. Sensitivity of predation on prey eaten after L_{opt} to lower steepness of stock-recruitment relationship. Baseline had a steepness = 0.8.

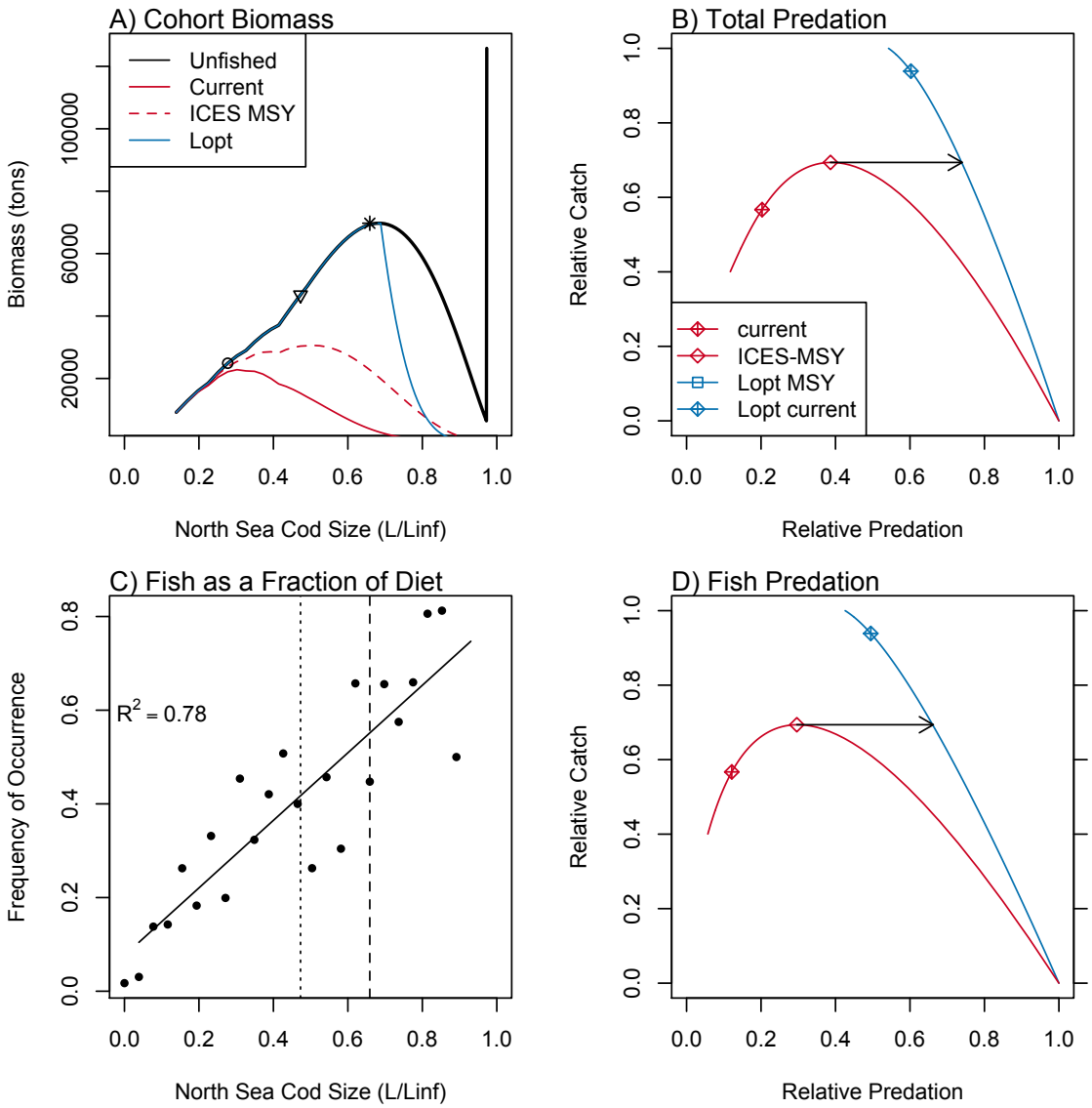

Fig B3. North Sea Cod A) cohort biomass, B) total predation, and D) fish predation when age-dependent natural mortality in Table A3 was used in the simulation.

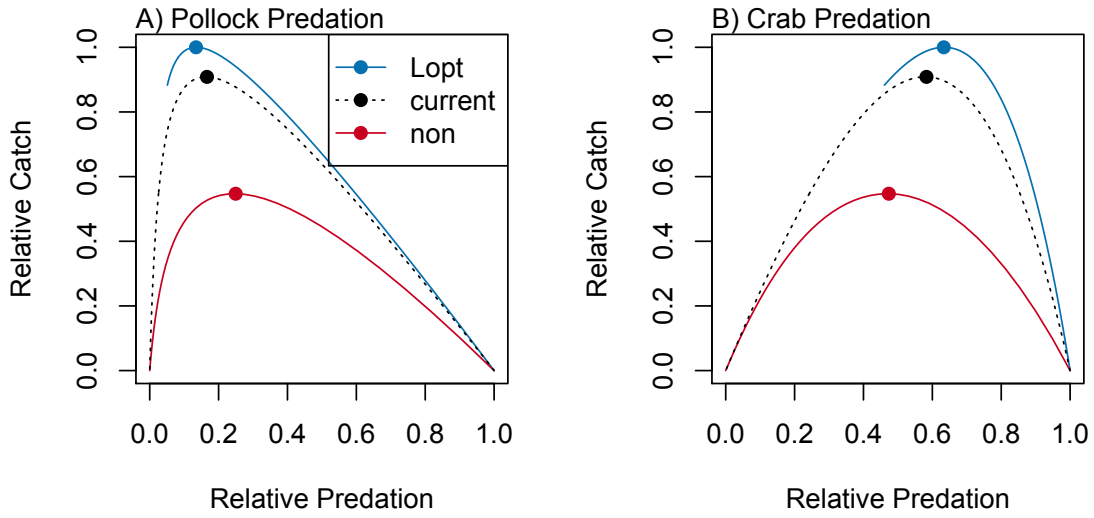

Figure B4. Pacific Cod predation on A) pollock, and B) crab by cod fished with Steepness = 0.8. Closed circles represent fishing at MSY.

II: Recovery of predators in a marine reserve alters size-dependent prey mortality

Abstract

By increasing the density, size, and biomass of targeted predators, marine reserves are thought to restore predator-prey interactions and lead to trophic cascades. However these indirect effects are not always observed and often lag significantly behind effects on target species. One mechanism that may help explain this lag is size-dependent predation, where fishing for predators can effectively truncate predator size structure and thus allow certain prey to achieve a size refuge from predation. Although predator densities are often observed to increase inside marine reserves in the absence of fishing, these invulnerable prey can still continue to avoid predation and prevent trophic cascades until they die from other causes or until sufficient numbers of predators grow to be large enough to consume them. To better predict the trajectories of community change in marine reserves, it is necessary to understand the size-dependence of important predator-prey interactions and how fishing affects predator abundance and size structure. We first examined how the interaction between urchins and one of their important predators, California Sheephead, depends on body size. We then identified whether size thresholds exist below which sheephead do not eat urchins and examined how the predator-prey interaction varied with urchin size. We finally examined how differences in sheephead population structure inside/outside of a marine reserve at Catalina Island translated into differences in size-specific urchin mortality rates. We found that reserves were characterized by elevated sheephead densities, particularly those individuals >20 cm in length—the threshold size at which sheephead begin to eat urchins of any size. In addition, larger critical sizes of

sheephead were required to successfully attack and consume larger urchins. Large sheephead also preferentially targeted the largest urchins, likely due to the higher caloric value of their gonads. In experiments testing predation rates on two urchin species, shorter-spined purple urchins were attacked more frequently than larger-spined red urchins, especially at the largest test diameters. As a result of these size-specific patterns in the interaction between sheephead and urchins, and the differences in size structure observed in the reserve, urchin mortality rates were higher in the reserve for both purple and red urchins. Because fewer sheephead were capable of eating large urchins, mortality decreased with urchin size. Mortality on the largest urchins was disproportionately reduced in the fished areas, except for large red urchins that were consumed at low levels in both the fished and reserve areas. Truncation of the sheephead size structure due to fishing will result in reductions in urchin mortality rates, particularly for the largest urchins. If such truncations in sheephead size structure are maintained for long enough, urchins may be able to achieve a size escape that could serve to delay indirect positive effects of reserve protection on urchin grazing pressure and macroalgal cover. Ultimately, by restoring predator size structure, reserves may serve to enhance the resilience of southern California kelp forests.

A. Introduction

Recent studies of marine reserves demonstrate that species targeted by fishing consistently experience increases in density, body size, and biomass compared to nearby fished areas (Lester et al. 2009). Because many targeted species are predators, marine reserves are thought to restore key predator-prey interactions, and thereby lead to trophic cascades in which increases in predator abundance cause a decline in herbivore populations, thereby allowing communities of primary producers to flourish (Pinnegar et al. 2000). Many studies have attempted to demonstrate such indirect effects of protection, but the results have been equivocal (Micheli et al. 2004). In addition, indirect effects often lag significantly behind the direct effects of marine reserve protection (Babcock et al. 2010). To predict better how communities will respond to both fishing and protection in marine reserves, we need a more mechanistic understanding of how predator-prey interactions are affected by changes in both predator abundance and body size.

Much of the evidence supporting the occurrence of trophic cascades in response to the establishment of marine reserves or the recovery of predator populations involves herbivorous sea urchin prey (Pinnegar et al. 2000, Babcock et al. 2010). Where predator abundance is low and sea urchin abundance is high, sea urchins can overgraze algae, causing a phase shift to an urchin barren devoid of macroalgae and much of the associated diversity (Steneck et al. 2002, Graham 2004). Unlike other consumers that drive themselves extinct from a patch if they deplete their resources (Hilborn 1975, Murdoch and Oaten 1975, Hastings 1977, Murdoch 1977), urchins can switch to grazing on crustose coralline algae (Harrold and Reed 1985) and other low quality resources after they deplete their macroalgal resource or even resorb somatic tissue and shrink in size

(Ebert 1967, 2008). As a result, urchins can survive at extremely high densities for decades, which can drive phase shifts that are stable for many years (Filbee-Dexter and Scheibling 2014). High densities of urchins can create a positive feedback loop that restricts the capacity for macroalgae to successfully reestablish in urchin barrens (Baskett and Salomon 2010).

Where marine reserves have been established, changes in urchin abundance often greatly lag behind the recovery of their predators, sometimes by decades (Babcock et al. 2010). One mechanism suggested by Babcock et al. (2010) for such time lags is size-dependent predation. In the absence of predators, urchins can grow to very large sizes that are invulnerable to predation when predators return, at least until the protected predators grow sufficiently large (Babcock et al. 2010). As a result, understanding the size-dependence of the interactions between predators and urchins is critical to making accurate predictions of the trajectory of recovery following the establishment of marine reserves and the consequences of management actions that affect predator size structure.

In southern California, the California Sheephead (*Semicossyphus pulcher*) and spiny lobster (*Panulirus interruptus*) are both important predators of sea urchins (*Strongylocentrotus purpuratus* and *Mesocentrotus franciscanus*) in kelp forests. The presence of both predators is thought to have contributed to the relative resiliency of southern California kelp forests to the extirpation of sea otters in the 1800s, while kelp forests elsewhere without complementary predators were converted to urchin barrens (Pinnegar et al. 2000, Steneck et al. 2002). The link between sheephead and urchins was corroborated by experimental work showing that removal of sheephead from a site on San Nicolas Island resulted in a 26% increase in urchin numbers and an increase in the

proportion of urchins occupying exposed habitats (Cowen 1983). However, the role of sheephead in controlling urchin abundance may be drastically reduced in some locations due to intense human harvesting (Dayton et al. 1998). Here we focus on the effects of fishing for sheephead and their subsequent recovery in marine reserves on urchin demographics.

Sheephead have been a prime target of recreational fisheries since at least the 1950s, and landings surged in the 1980s (Alonzo et al. 2004). Starting in 1990, commercial landings boomed with the advent of a trap fishery for the live fish market (Alonzo et al. 2004). Since the live fish fishery targets small, "plate-sized" fish (Loke-Smith 2011), many sheephead were caught before they reached maturity or could change sex to become males (Dayton et al. 1998). By 2004, when the first stock assessment was completed, the stock was well below management targets, with mature biomass estimated to be at 20% of the unfished level (Alonzo et al. 2004). In addition, intense fishing truncated the size distribution of sheephead populations, in concert with shifts in life history traits such as declines in the size at sex change (Hamilton et al. 2007). If the interaction between sheephead and urchins depends on size, this truncation in size structure has the potential to affect both the viability of the sheephead population as well as their functional role as urchin predators in kelp forest systems.

Although their life history as a sex-changing fish may make them more vulnerable to fishing, the high site fidelity (Topping et al. 2006) and small home range of sheephead (Topping et al. 2005) make them more likely to benefit from protection in marine reserves than other more mobile predators. A recent study reported that sheephead density, size, and biomass increased in new reserves in the northern Channel Islands

(Hamilton and Caselle 2015) after 10 years of protection and that urchin abundance is lower at sites with greater sheephead biomass. Sheephead densities are also elevated in a small reserve on Catalina Islands (established in 1988; Froeschke et al. 2006). However, this high density was not due to a comparable increase across sheephead size classes but rather due to a higher density of adult sheephead, while juvenile densities remained constant. As a result, reserve protection has resulted in changes in sheephead population structure, in parallel with density.

In the context of these shifts in sheephead body size, we evaluate the consequences for the functional role of sheephead as urchin predators. We first examine how the interaction between sheephead and urchins depends on body size. We identify whether a threshold size exists below which sheephead do not consume urchins, and we evaluate how this threshold varies as a function of urchin size class. We finally examine how these changes in sheephead size structure and density are translated into differences in urchin predation rates, for urchins of different size classes and species.

B. Methods

1. Study Species

California sheephead are large temperate wrasses (family Labridae) occupying inshore rocky reefs and kelp beds from Point Conception to Baja California (Caselle et al. 2011). Sheephead display high site fidelity (Topping et al. 2006) with small home ranges (0.3 to 1.2 km alongshore distance). Sheephead are protogynous hermaphrodites that begin life as female and change sex to male at large sizes (Warner 1975).

Sheephead prey upon two herbivorous urchin species that occupy rocky reefs in southern California: the purple urchin *S. purpuratus,* and the red urchin *M.* fransciscanus. For a given test diameter, red urchins have longer spines, and spine length increases more quickly with size. Both factors increase the relative handling time of red versus purple urchins for predators. The fishery for red urchin roe is one of the most valuable in California (Kalvass et al. 2004), while purple urchins do not currently support a commercial fishery (Parker and Ebert 2004). Both urchin species preferentially graze macroalgae, including the giant kelp *Macrocystis pyrifera*, but they will shift to coralline algae when other algal resources are scarce (Harrold and Reed 1985).

2. Surveys and Predation Trials

Sheephead surveys and predation trials were conducted at three sites inside the Catalina Marine Science Center Reserve (Chalk Cliffs 33° 26′ 40″N, 118° 29′ 19″W; Intake Pipes 33° 26′ 49″N, 118° 29′ 06″W; Pumpernickle 33° 26′ 54″N, 118° 28′ 48″W) and three sites in the fished area outside the protection of the reserve (Lion's Head 33° 27′ 13″N, 118° 30′ 05″W; Isthmus Reef 33° 26′ 54″N, 118° 29′ 22″W; Bird Rock 33° 27′ 05″N, 118° 29′ 19″W; Fig. 1). The no-take marine reserve was established in 1988 and encompasses 0.13 km^2 (Topping et al. 2006). Sites consisted of high relief (>1m) boulder and rock cobble habitat with giant kelp (*Macrocystis pyrifera)* between 5 and 20 m depth.

Sheephead abundance and size distributions were quantified using SCUBA surveys on five 30m x 2m transects conducted in two reef zones (the inner (~10m depth) and outer (~14.5m depth) edges of the kelp bed at each site) in August 2010 and August 2011. Sizes were estimated visually to the nearest cm (total length [TL]). In August 2010

we used predation trials to examine size-specific predation on sea urchin prey. We examined predation on two species of sea urchin: red (*M. franciscanus*) and purple (*S. purpuratus*). Urchins were collected at each of the six sites to test whether predation was dependent on sheephead size, urchin size, or urchin species identity. Each urchin was measured and assigned into one of three size classes: small (20-35mm test diameter [TD]), medium (35-50mm), and large (50-70mm). Urchins were held in tanks of flowing seawater at the USC Wrigley Marine Science Center for 24 hours. Predation trials consisted of placing $n = 15$ urchins of each of the two species and three size classes within three 1 m^2 quadrats (30 total urchins per quadrat with separate quadrats for each size class but mixed for each species) on rocky substrate in each habitat. Quadrats were used to visually identify the area containing the transplanted urchins and were located approximately 1m from each other. Divers then observed sheephead naturally attacking and consuming urchins for a 30 minute trial. The length of each sheephead observed to attack an urchin was estimated visually to the nearest cm for smaller sheephead and within 5cm size bins for sheephead larger than 40cm. Encounters were recorded when a sheephead attempted to attack a single urchin within the quadrat. The outcome of each encounter between sheephead and urchins was recorded as a success if it resulted in the consumption of an urchin or a failure if the attack was unsuccessful. After the 30 min predation trial, all surviving urchins of the three size classes and species were recollected and re-measured.

3. Statistical Analyses

The total density, and the density of small (<20cm) and large (>20cm) sheephead inside and outside of the reserve were compared using nested ANOVA (with site nested within reserve status) in R (R Core Team 2015). Sheephead biomass was calculated from the observed size distribution in total length (cm) using the length-weight relationship in Williams et al. (2013; TL=1.207SL+0.604; $W(g)=aSL(cm)^b$ where $a=8.45*10^{-5}$, b=2.80). Biomass differences between fished and reserve areas were analyzed in the same way as density.

The difference between the size distribution of sheephead observed in surveys and those observed eating urchins in feeding trials was analyzed using Monte Carlo simulations (n = 1,000) of the Kolmogorov-Smirnov test with the ks.boot function in the Matching R package (Sekhon 2011). The probability of success given an encounter was assessed as a function of sheephead and urchin size using a generalized linear model with binomial errors. An encounter was recorded when a sheephead attempted to attack an urchin. Successful encounters resulted in the sheephead consuming the urchin. We used the model to calculate the size at which the predicted probability of a successful encounter was >10%, which we defined as our threshold size. We also calculated the size at which 50% of encounters resulted in successful urchin consumption.

Among successful urchin attacks, the overall size preferences as well as the relative preference for urchin species and size class as a function of sheephead size were assessed using a multinomial logistic regression with the multinom function in the nnet package in R (Venables and Ripley 2002). Sheephead <25 cm were only observed successfully attacking an urchin once and were therefore removed from the analysis for sheephead preferences.

Mortality rates for urchins in each size class for red and purple urchins inside and outside of the reserve were compared with a three-way ANOVA with urchin size, species, and reserve status and their interaction as factors. Differences in mortality between size classes were assessed using Tukey HSD comparisons.

C. Results

Sheephead were 26% more abundant overall in the reserve with significant variation by site (status $F_{1,112} = 7.642$, $p = 0.007$; status(site) $F_{5,112} = 5.802$, $p < 0.001$ Fig. 2). The size distribution was distinctly different in the reserve. Sheephead smaller than 20 cm were equally abundant inside and outside of the reserve (status $F_{1,84} = 0.69$, $p = 0.409$, status(site) $F_{5,84} = 6.728$, $p < 0.001$). In contrast, sheephead ≥20 cm were 53% more abundant in the reserve (status $F_{1,106} = 17.846$, $p < 0.001$, status(site) $F_{5,101} = 2.274$, $p = 0.052$). As a result, mean sheephead size was 4 cm greater and total biomass was 2x higher in the reserve (size: $t = 3.0461$, $p = 0.002$; biomass: status $F_{1,112} = 24.587$, $p < 0.001$; status(site) $F_{1,112} = 2.186$, $p = 0.0607$).

The sizes of sheephead observed eating both red and purple urchins were skewed toward larger sizes relative to the surveyed population (bootstrap K-S test, $D = 0.49$ and $p < 0.001$ for red urchins; $D = 0.51$ and $p < 0.001$ for purple urchins; Fig. 3). Sheephead smaller than 20 cm were not observed to consume urchins, despite the high relative abundance of small sheephead. In contrast, sheephead larger than 25 cm were disproportionately involved as urchin predators.

The probability of predation success as a function of sheephead size did not vary among the urchin species (Wald $Z = -0.49$, $p = 0.62$ for small urchins, Wald $Z = -0.11$,

p=0.729 for medium urchins, and Wald Z=0.713, p=0.476 for large urchins). Thus, results were pooled across urchin species. Sheephead size was a significant predictor of the probability of success given encounters with urchins of all urchin size classes (Table 1; Fig. 4). Once sheephead were large enough to begin eating urchins, all sizes were capable of consuming small urchins (Fig. 4A). Yet, as urchin size increased, the threshold sheephead size increased. For medium urchins, 10% of encounters were successful for sheephead > 24 cm, and a size of 35cm was required for 50% of encounters to be successful. For large urchins, 10% of attempts were successful for sheephead > 29cm, while only sheephead sizes > 43cm were successful in more than half of their attempts (Fig. 4B and 4C; Table 1).

The relative consumption of the different urchin size classes varied with sheephead size (Fig. 5). At the onset of including urchins in the diet at ~20 cm, sheephead only consumed small urchins. Small urchins declined to 50% of the urchins consumed at a sheephead length of 38 cm, as medium urchins were gradually added into the diet (Fig. 5). The largest sheephead preferentially targeted even larger urchins, and at a size > 53cm, 50% of their diet was comprised of large urchins (Fig. 5). As a result, the risk for medium and large urchins relative to small urchins increased substantially as sheephead size increased (Table 2). Purple urchins were preferentially targeted, especially by the large sheephead size classes, which preferred larger urchins (Fig. 6). Medium and large reds were therefore at a lower risk of being consumed than purple urchins in the same size class (Table 2).

Consistent with the above differential effects of sheephead size classes, urchin mortality was higher inside the reserves ($F_{1,136}$=32.902, p <0.001) compared to the fished

area outside (Fig. 7). Purple urchins were consumed at a greater rate than red urchins ($F_{1,136}$=7.735, p=0.006). Because fewer sheephead were capable of consuming large urchins, mortality decreased with urchin size for both urchin species ($F_{2,136}$=17.867, p<0.001). There was a marginally significant interaction between species and reserve status ($F_{1,136}$=3.656, p-0.058), due to the lack of difference between reserves and fished areas for large red urchins. There was also a marginally significant interaction between urchin size and reserve status ($F_{2,136}$=2.359, p=0.098) due to the greater reduction in mortality in fished areas for larger urchins. Mortality on small purple urchins was reduced by 2-fold, while mortality on medium and large urchins was reduced by more than a factor of 4. Similar size-specific trends were observed with small and medium red urchins.

D. Discussion

The interaction between California Sheephead and sea urchins was strongly size dependent. Despite their high relative abundance, small sheephead were not involved in consuming urchins. No sheephead ate urchins of any size until they reached at least 20 cm. This size-dependent predator-prey interaction is likely controlled by the functional limitations of the crushing ability of the sheephead jaw, which is needed to break open a rigid urchin test, and likely increases with the size of the fish, similar to the closely-related Caribbean hogfish (Wainwright 1988, 1991). At small sizes, sheephead primarily consume bivalves (Hamilton et al. 2011). They add urchins into the diet as their crushing capacity increases as they grow in size. At the size threshold we found that urchins were added into the diet, sheephead ate only small urchins. To consume larger urchins required

ever larger sheephead. Interestingly, the threshold sheephead size required to consume large urchins is near the minimum size limit in the sheephead fishery (30 cm for the recreational fishery and 33cm for the commercial fishery), which has important management implications.

Large legal-sized sheephead consumed urchins at a rate disproportionate to their relative abundance. They also preferentially targeted large urchins, especially of the smaller-spined *S. purpuratus*. As a result of these size-dependent predation patterns, the higher abundance of large sheephead in the reserve led to higher urchin mortality. The relative increase in predation in the reserve was more pronounced for larger purple urchins. Although Behrens and Lafferty (2004) showed that urchin size distributions are dramatically different between fished and protected areas, this is the first experimental demonstration of the effects of reserve protection on size-specific urchin mortality rates in southern California kelp forests. The increased urchin mortality in reserves should lead to lower urchin abundance and fewer large reproductive individuals, reducing both grazing pressure and future reproductive output. As a result, the restoration of sheephead size structure and abundance in reserves may serve to enhance the resilience of kelp forest ecosystems. Indeed, urchin abundances are lower at sites inside the long-term marine reserve at Anacapa Island (established in 1978) compared to unprotected sites (Behrens and Lafferty 2004; Babcock et al. 2010). Over the thirty years of protection, urchin and kelp populations have been stable inside the reserve, while urchin abundance has doubled outside the reserve with concomitant declines in kelp abundance (Babcock et al. 2010). This suggests that protection for predators like sheephead inside reserves may increase predation on urchins, indirectly decrease grazing pressure on kelp and other

macroalgae, and therefore make it less likely for kelp forests to be converted to urchin barrens.

The size-dependent nature of the interaction between sheephead and urchins may also explain some of the lag in community responses to newly established marine reserves in southern California. Ten years after the establishment of many newer marine reserves in the northern Channel Islands, both sheephead densities and biomass were higher in reserves across the islands (Hamilton and Caselle 2015). Recovery of sheephead size structure is associated with a shift in sheephead diets towards greater consumption of urchins (Hamilton et al. 2014). Sites with higher sheephead biomass were associated with fewer urchins and higher quantities of fleshy macroalgae (Hamilton and Caselle 2015). Some sites that were urchin barrens prior to the establishment of marine reserves have successfully transitioned to kelp forests (Kushner et al. 2013, Sprague et al. 2013). However, on average, urchin density was higher in reserves on Santa Cruz, San Miguel, and Santa Rosa Islands than in fished areas for the same time period, particularly for purple urchins (Hamilton and Caselle 2015), and urchin barrens persist within some reserve sites, a decade after fishing on sheephead ceased (Sprague et al. 2013). As shown here, since sheephead do not eat urchins until they reach a critical size, there is an inevitable lag between reserve establishment and the potential for sheephead to significantly contstrain urchin populations.

Given the calls for ecosystem-based management (Heltzel et al. 2011), it will be important to consider how various management strategies affect the capacity for predator populations to regulate prey dynamics by altering predator size structure. Marine reserves have been shown to be one of the most effective tools to restore age and size structure of

targeted species (Berkeley 2006), and the results presented here suggest reserves can be particularly successful in restoring the benefits of unaltered predator-prey interactions. However, in those areas where fishing continues, the effect of alternative management approaches on predator abundance and size structure should be considered. Slot limits, in which fish are not caught until a minimum size limit, and are released above a certain size, are one potential option that could increase the age and size structure of the population when the slot is relatively narrow and release mortality of large fish is low (Berkeley 2006). Fisheries with slot limits allow fished populations to maintain a higher proportion of individuals in older/larger classes than fisheries that selectively target the largest size classes (Brunel and Piet 2013); however fishery yields may pay a cost to maintain these ecosystem benefits. Optimal decisions must therefore be based on the potential tradeoffs between the value of the fishery and the indirect benefits provided by the predator to the ecosystem.

Slot limits have been suggested as a way to improve the sustainability of the sheephead fishery by several authors (Hamilton et al. 2007, Loke-Smith et al. 2012), and they are currently being used in Australia for another sex-changing fish, barramundi – a protandrous hermaphrodite that begins life as male, matures, and then changes sex to mature female late in life, in order to maintain egg production by mature females (Milton et al. 1998). Because the main commercial fishery for sheephead utilizes traps that bring sheephead to the surface alive, slot limits may be a viable management option to maintain a greater fraction of large fish in the population if barotrauma and release mortality can be minimized. Since these live fish also decline in value as they grow too large for a plate, such a slot limit may also have limited economic impact on the fishery. Because

sheephead are a sex-changing fish in which truncation in size structure can result in skewed sex ratios and disruption in reproduction if sperm limitation occurs (Heppell et al. 2005, 2006), it may be possible to achieve win-win outcomes both by improving the sustainability of the sheephead fishery and enhancing the resilience of kelp forest ecosystems by increasing urchin predation. However, as the slot may result in increased targeting of females, it would be important to assess whether total reproductive output would be adversely affected.

From a holistic management point of view, increasing the proportion of large sheephead in the population and increasing their predation on urchins may come at the expense of the red sea urchin fishery. The red sea urchin fishery is one of California's most valuable, primarily exporting to the Japanese sushi market (Kalvass et al. 2004). In addition, unlike purple urchins, red urchins rarely form urchin barrens in southern California, so increasing predation on red urchins may not have the same ecosystem benefit. Although increased predation by sheephead may result in lower red urchin abundances, the preferential consumption of purple urchins by sheephead observed in this study may ameliorate competition between the two species that could enhance gonad production in the red urchins (Claisse et al. 2013). Since it is these gonads that are the object of the fishery, the decline in numbers of urchins may be mediated by an increase in the value of each individual urchin. Therefore, the net outcome for both fisheries yields and ecosystem objectives may be positive by restoring sheephead size structure, but this warrants further investigation.

E. Conclusion

The size-dependent interaction between urchins and their predators will influence the relative effect of fisheries management strategies on the capacity for predators to regulate urchin populations as well as the trajectory of recovery in marine reserves. Marine reserves are particularly successful in restoring the interaction between sheephead and urchins, though delays in recovery of kelp forest ecosystems may be observed until sufficient numbers of sheephead are large enough to be effective urchin predators. Slot limits could be explored as an alternative where it is desired for fishing to continue. Whichever management method is used, increasing the proportion of large individuals in the sheephead population may increase the resilience of the kelp forest habitats in which they serve a key role.

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G. Tables

Table 1. Results of logistic regression for predation success as a function of sheephead size. For a one unit increase in sheephead size, the odds of successful predation increase by a factor of the odds ratio.

Urchin Size	Odds Ratio (95% CI)	Wald Z	Length at 10% Success (cm)	Length at 50% Success (cm)
S	1.08 (1.02, 1.15)	2.641**	0	13
M	1.22 (1.14, 1.31)	5.936***	24	35
L	1.17 (1.11, 1.25)	5.398***	29	43

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 2. Relative risk is the ratio of the probability of an urchin being eaten in one category over the probability of being eaten in the baseline category (here a small purple urchin). As sheephead size increased, the relative risk for medium and large urchins increased relative to that of small urchins. Larger red urchins had lower relative risk than their purple size-matched counterparts.

Urchin Size	Relative Risk Ratio (relative to small purple urchin)		Wald Z	
	Sheephead Size	Urchin Species (P→R)	Sheephead Size	Urchin Species (P→R)
M	1.217	0.489	8.06***	-2.64**
L	1.29	0.33	8.95***	-2.97**

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

H. Figures

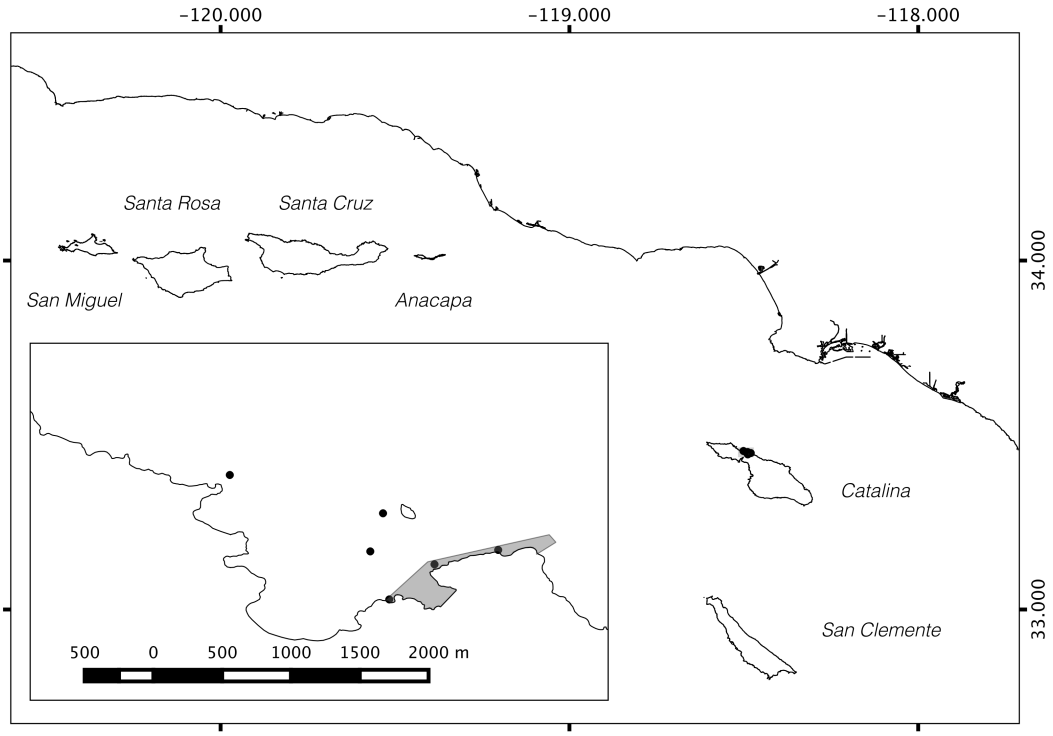

Figure 1. Greater study region in the southern California Bight, depicting the offshore Channel Islands (note: Santa Barbara and San Nicolas Islands not shown). Black shaded rectangle highlights location of specific study region on Catalina Island. Inset: Filled black circles represent sites of surveys and predation trials at Catalina Island. Gray shaded area is the Catalina Marine Science Center Reserve.

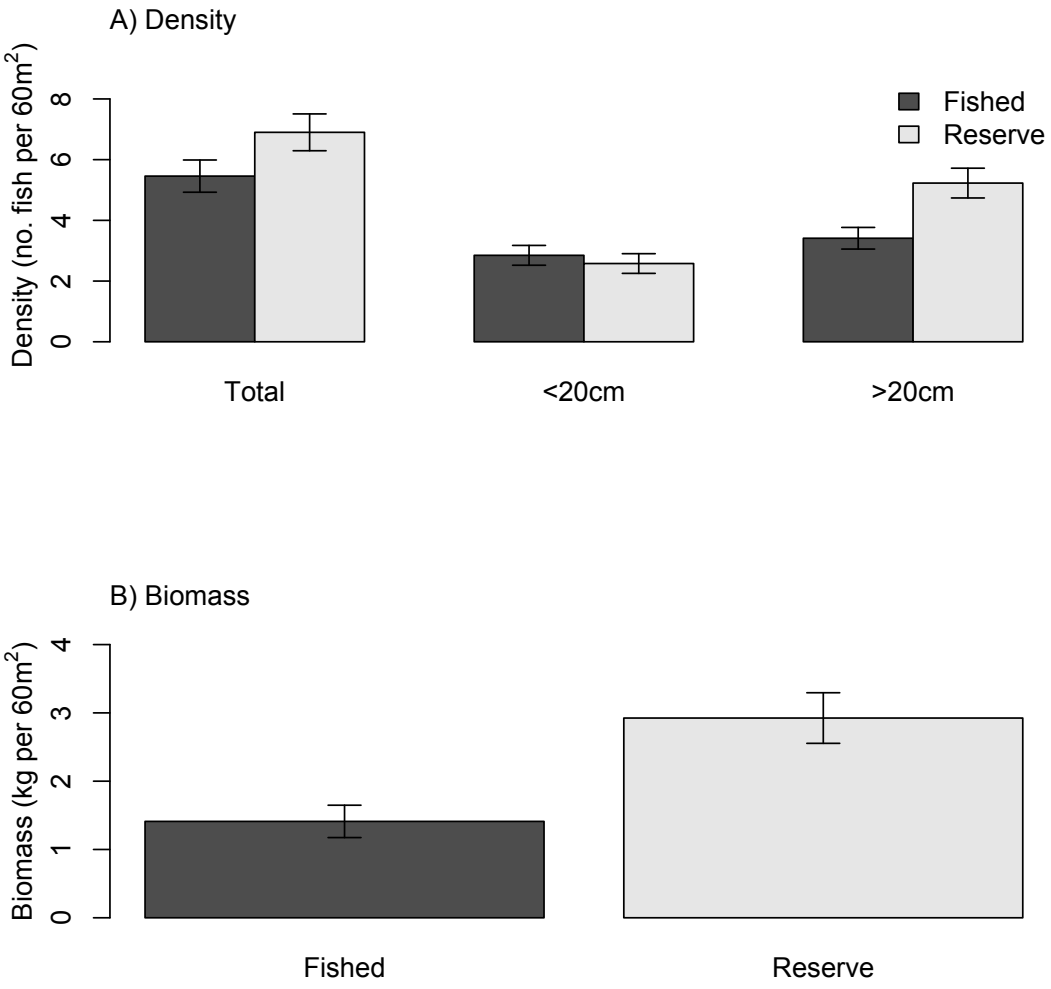

Figure 2. A) Differences in the density of sheephead (number of fish per 60m^2 transect) inside and outside of the reserve. Shown are total density, sheephead < 20cm TL, and sheephead > 20cm TL. B) Total biomass inside and outside of the reserve (kg per 60m^2).

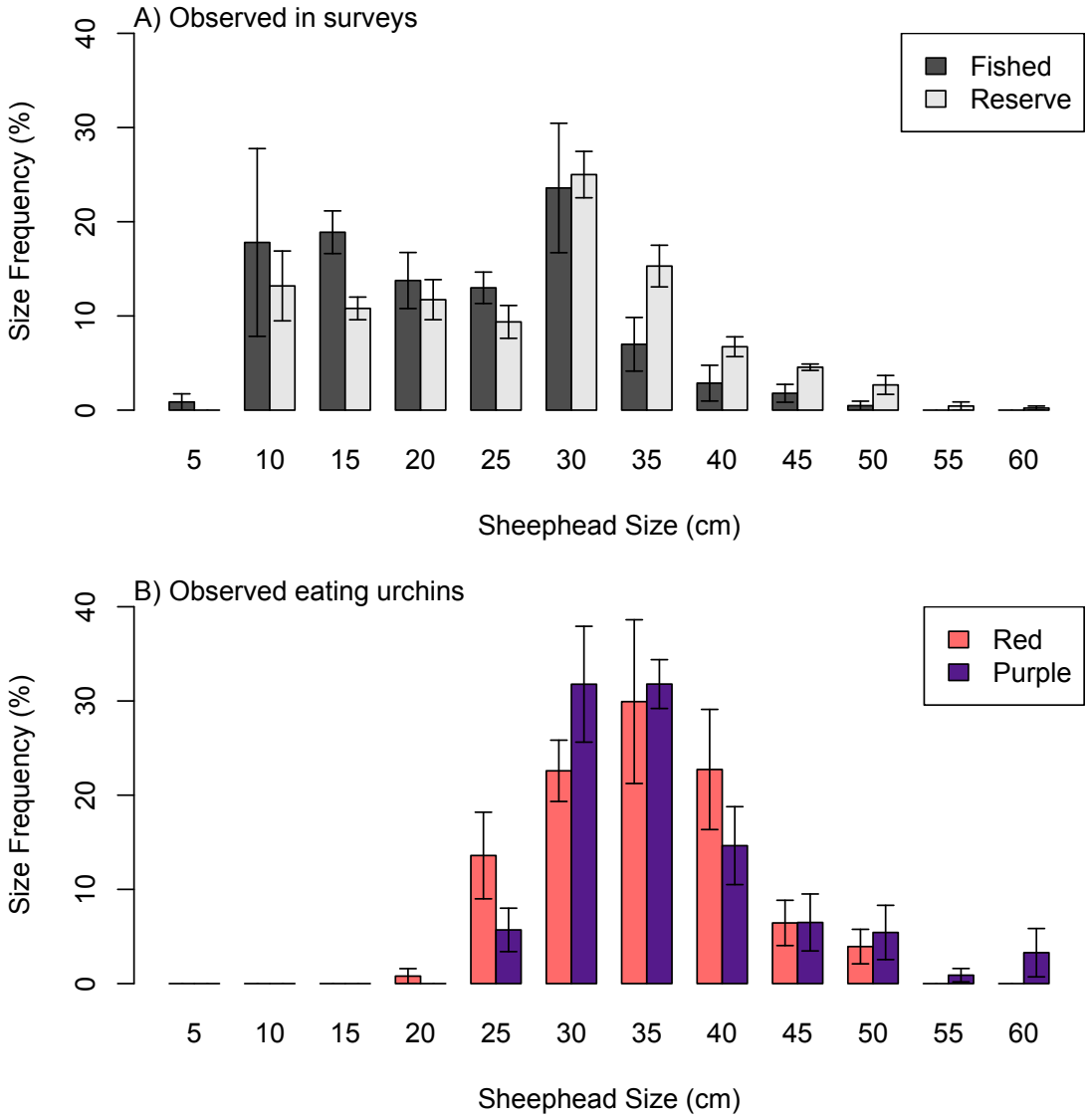

Figure 3. Size frequency (%) distribution of sheephead A) observed in surveys and those eating B) red or purple urchins in predation trails.

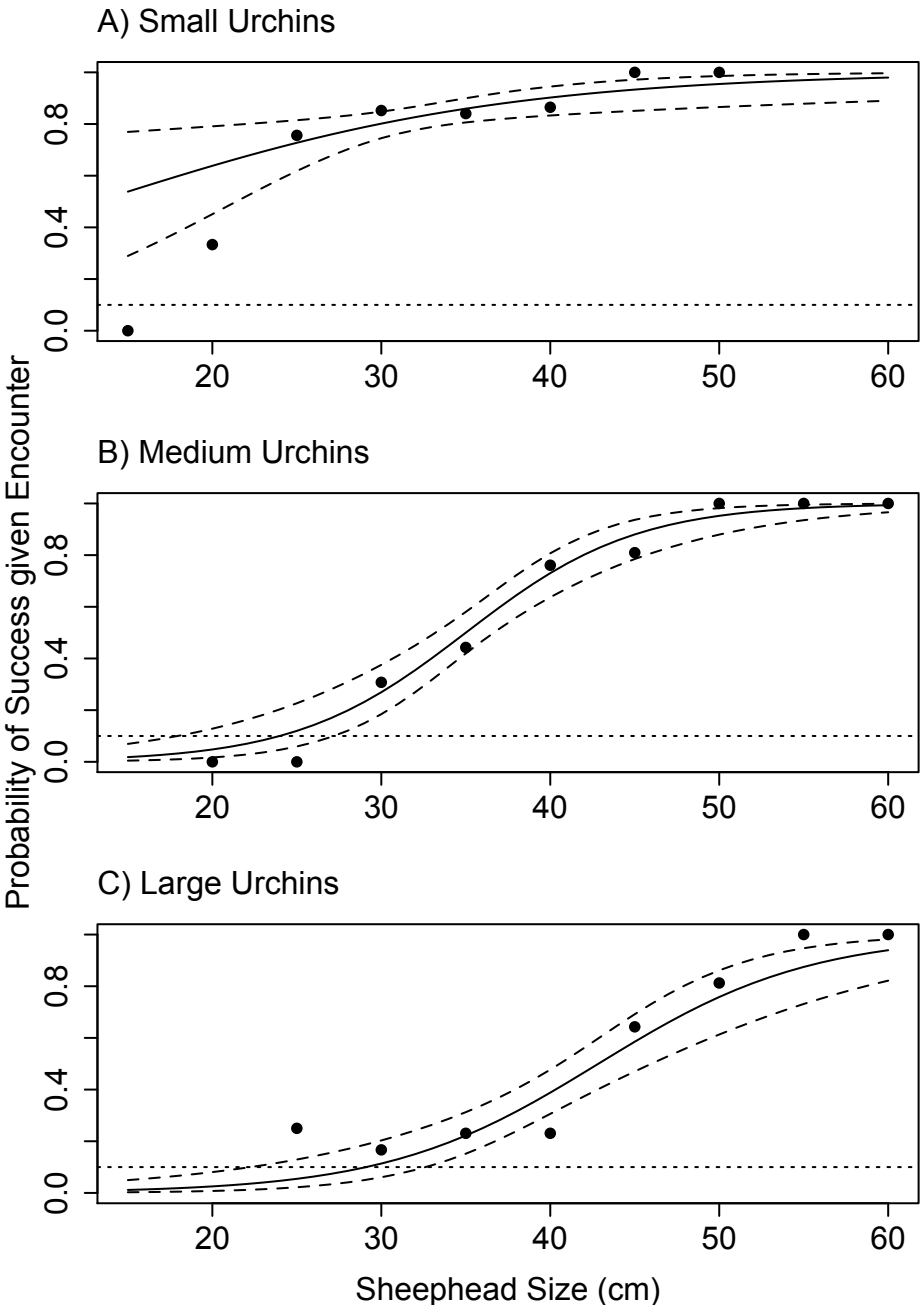

Figure 4. Probability of successfully eating an urchin given an encounter during the experimental feeding trials. A) small urchins (20-35mm TD), B) medium urchins (35-50mm), and C) large urchins (50-70mm). Closed circles represent the observed fraction of successful encounters, and lines represent that predicted from a generalized linear model with a binomial error distribution. Dashed lines are the 95% confidence intervals on the prediction. Dotted lines represent a 50% success rate.

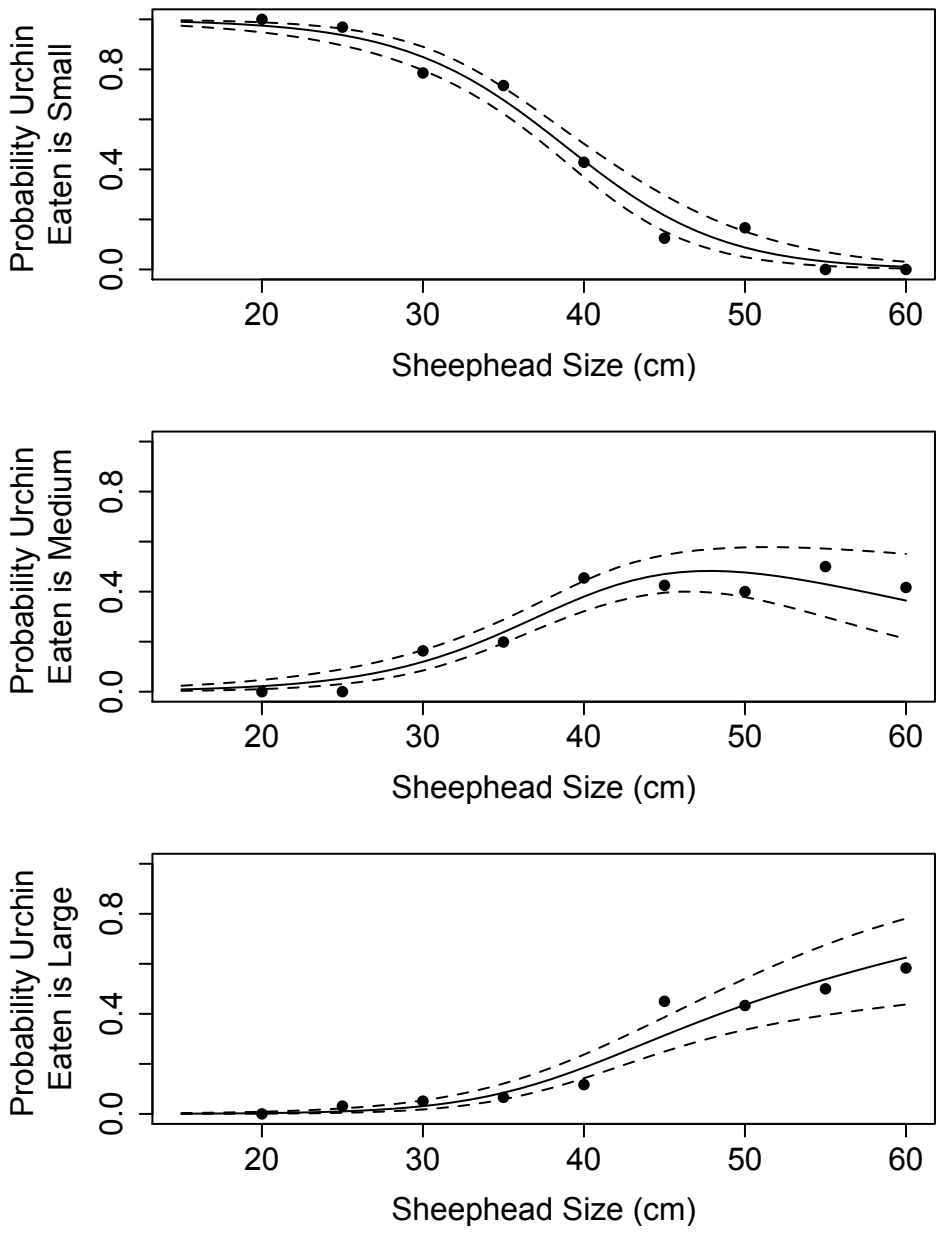

Figure 5. Observed proportion of successful attacks on each urchin size class of the total urchins consumed by a given sheephead size (filled circles). Mean (solid line) and 95% confidence intervals (dashed lines) for the predicted proportion of successful attacks on each urchin size class as a function of sheephead size.

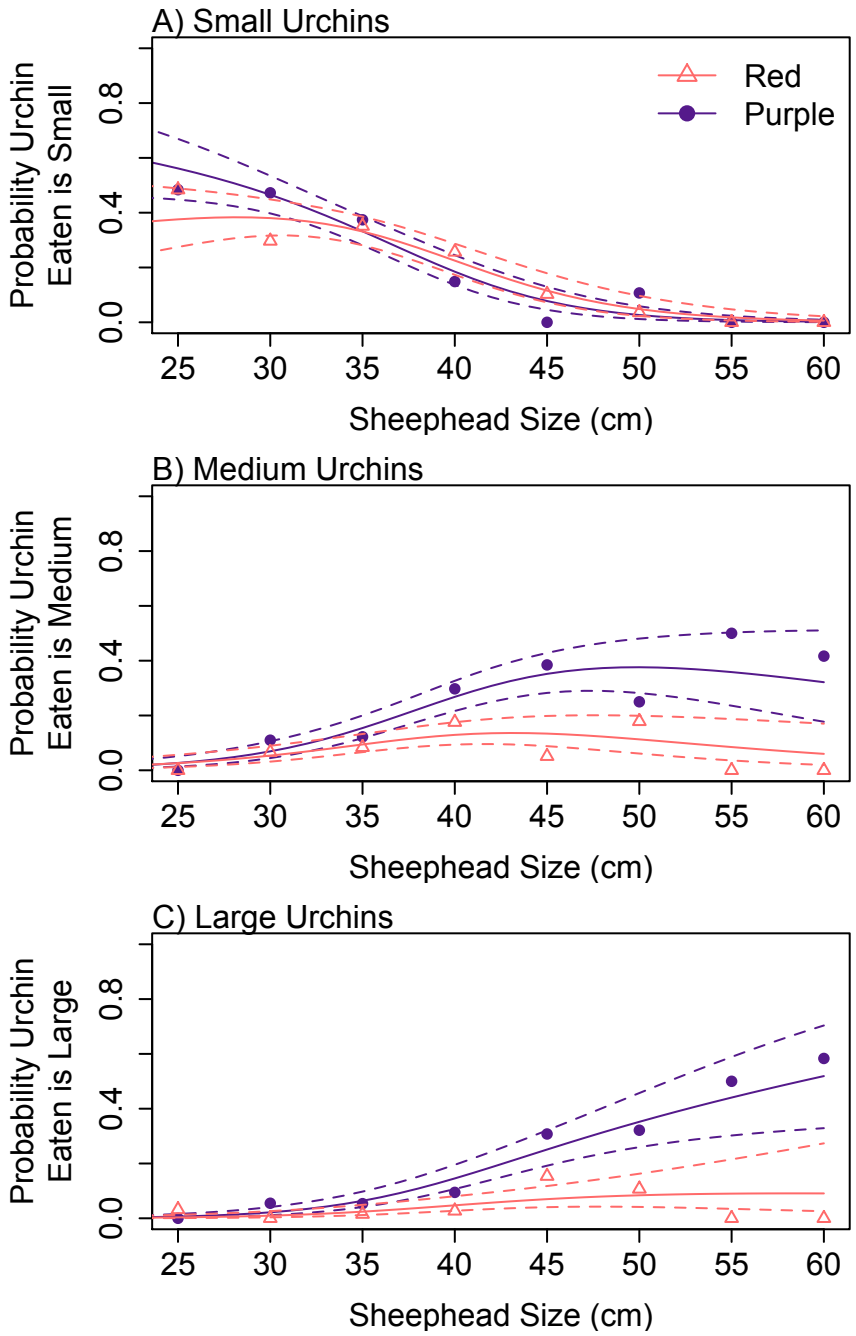

Figure 6. Observed proportion of successful attacks on each urchin size class for red (open red triangles) and purple (filled purple circles) urchins by sheephead size group. The mean (solid lines) and 95% confidence intervals (dashed lines) of predicted proportion from the multinomial model.

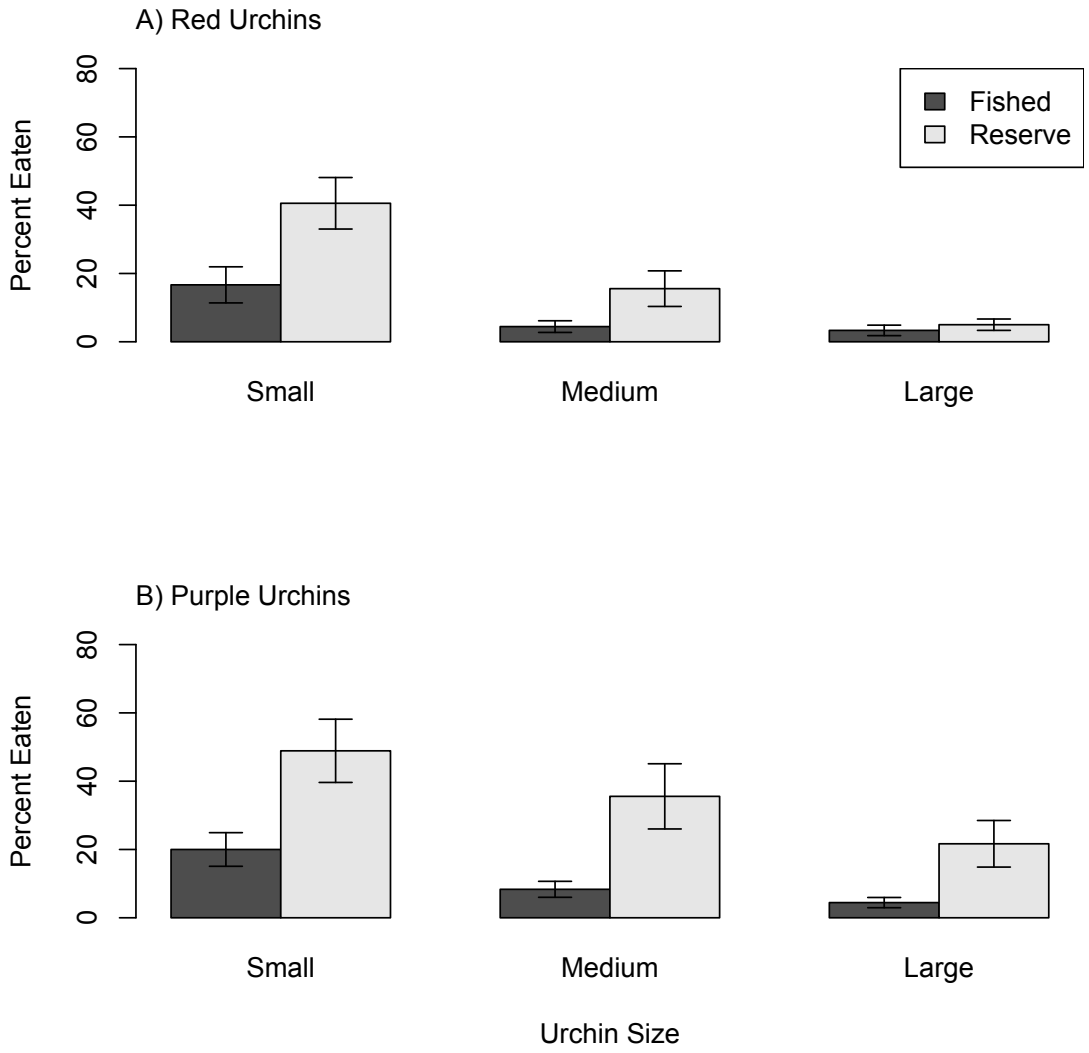

Figure 7. Size-specific urchin mortality inside and outside of the marine reserve for A) red urchins and B) purple urchins during 30 minute feeding trial.

III. Spatial variation in predator demography affects top-down control of prey populations and the likelihood of prey size refugia

Abstract

Body size is a plastic trait subject to variation due to environmental conditions as well as anthropogenic factors such as size-selective harvest. Because predators may shift both prey species as well as prey size classes within a species as they grow, truncation in predator body size distributions has the potential to eliminate predation on prey eaten late in life history. Where prey eaten late in life history are large individuals of the same prey species, the absence of large predators may create size refugia for large prey individuals that can disrupt top-down control on prey populations. However, unlike the scenario in which large predators eat different species where small predators have no capacity to compensate, high predation rates on small prey size classes by abundant small predators may prevent this outcome.

In this study, we examine how variation in predator body size distributions and biomass affects the likelihood of size escapes in situations where predators begin eating herbivorous sea urchins at some threshold size and thereafter consume increasingly larger urchins as they themselves grow. We focus on California sheephead, an important urchin predator in Southern California kelp forests that exhibits dramatic variation in both body size and abundance across its range, often achieving slower growth and smaller maximum sizes but higher biomass in the south of its range. We use sheephead and urchin population models to evaluate the consequences of smaller predator body size on top-down control of urchin populations in two scenarios: 1) when overall predator abundance is the same as the population with larger body size, and 2) when predator biomass is the same.

With the same numbers of predators, the absence of large predators reduced urchin consumption by 75%, leading to a doubling in urchin abundance and a release of the largest urchins. However, when sheephead biomass was maintained, the absence of large sheephead did not lead to greater urchin abundance, despite lower predation rates overall and much lower predation on large urchins. Higher predation rates on the smallest urchin size classes served as a bottleneck that kept total urchin population at similar levels and prevented a size escape for the largest urchins. With slower urchin growth rates, the capacity for the sheephead population without large sheephead to maintain top-down control was even greater than the population with large maximum size. The opposite was true for fast urchin growth rates. This suggests that where predators switch prey size classes in the same species, the loss of the largest individuals does not inherently result in weaker top-down control, if biomass is maintained (i.e. through high recruitment).

This variation in demography also affected the degree to which predator abundance and size was reduced by fishing with the current size limit, thereby affecting the capacity for top-down control on urchin populations. Because a greater fraction of the sheephead population with large maximum size was vulnerable to fishing with the current size limit, urchin consumption was reduced to a greater extent. However, because overall urchin abundance was most sensitive to changes in predation on small urchins, the greater reduction in predation on the small urchins due to fishing the population with small sheephead body size led to a greater release in the urchin population due to fishing.

A. Introduction

Body size determines many important ecological traits that affect the role of a species in a food web and the functioning of ecosystems (Woodward et al. 2005). In turn, the maximum size of an organism is known to be influenced by the environment. Individuals reach smaller asymptotic sizes where food availability is limited or in environments that are physiologically stressful (Sebens 1987). In addition, populations with higher densities of conspecifics and greater intra-specific competition for resources grow more slowly and achieve smaller maximum sizes (Lorenzen and Enberg 2002). Warming due to climate change has also been shown to shift the body size distributions of the community towards smaller individuals (Daufresne et al. 2009, Dossena et al. 2012, Cheung et al. 2012). As a result, current and future geographical variation in environmental characteristics may drive substantial differences in body size distributions that can affect food webs.

Size-selective harvest is also a strong determinant of body size distributions. Fisheries that target large size classes cause the greatest deviation in size structure from unfished levels (Law et al. 2012) by reducing the relative abundance of large individuals. However, the increased mortality imposed by non-selective fisheries or those that target the small size classes can also lead to truncations in size distributions by making it less likely that individuals will survive to large sizes.

Where variation in body size occurs in predator populations, differences in body size distributions have the potential to alter the strength of their interactions with their prey. Because larger predators can move more quickly to capture mobile prey (Christensen 1996), have larger gape sizes and stronger jaws that can handle larger, more

robust prey (Wainwright 1987), and have higher metabolic demands (Brown et al. 2004), predator body size often drives variation in both the amount but also the species and sizes of prey consumed. As a result, differences in predator body size distributions can cascade to affect the relative mortality rates of a particular prey species and size class. Ontogenetic or size-based shifts in diet are particularly common in aquatic systems (Werner and Gilliam 1984), and therefore marine and freshwater food webs may be susceptible to disruption due to changes in predator body size distributions.

Reductions in predator body size alone may be sufficient to cause cascading changes in the ecosystem. Shackell et al. (2010) observed a 60% decline in mean body mass in the oceanic ecosystem on the Western Scotian Shelf since the 1970s, such that the size of the individuals in each trophic level today is the same as the one below it in 1970. As a result, despite similar levels of aggregate predator biomass, prey biomass increased 300%. This suggests that reductions in predator body size, even in the absence of changes in biomass, have the capacity to alter top-down regulation of prey populations.

The extent to which alterations in predator body size distributions lead to changes in ecosystem function will depend on the degree to which diet changes with body size. Marine predators, such as fish, often display distinct diet shifts as they grow through several orders of magnitude in size in their lifetimes (Werner and Gilliam 1984, de Roos and Persson 2013) with adjacent size classes of predators often sharing few prey resources. These ontogenetic changes in diet can involve shifts in prey species composition as well as size. Maximum and mean prey size eaten typically increase as predators grow (Scharf et al. 2000). Where prey of different sizes represent different

species, truncations in predator size structure may cause reductions in consumption of prey eaten late in life (Chapter 1) and could result in releasing that prey from top-down control. Such dramatic prey switching at large sizes has been observed in some species, such as Pacific cod in the Gulf of Alaska (Urban 2012). Increases in the size of prey consumed as a function of increasing predator body size is ubiquitous in marine systems, but the ecosystem consequences of fishing-induced changes in the size structure of predators with a diet shift from one prey size to another, are less clear.

One way in which truncation in size structure for predators with this type of diet shift may affect ecosystems is through the creation of size refugia, in which prey become invulnerable to predation over a certain size. The absence of large predators due to geographic variation in demography or differences in harvest intensity or fisheries size-selectivity may make it more likely that their prey will achieve a size escape from predation. Such invulnerability can induce alternative community states and prevent trophic cascades (Ling et al. 2009). For example, the exclusion of predatory seastars for 5 years from intertidal beds in Washington allowed their prey to achieve a size refuge, and these mussels persisted after seastar recolonization for an additional 30 years (Paine and Trimble 2004), preventing coexistence of algae. Similarly, the introduction of largemouth bass in lakes did not cascade down to affect phytoplankton abundance in lakes which had large-bodied intermediate consumers that exceeded the gape limitation of the predator (Nowlin et al. 2006). Likewise, a trophic cascade following increased predator densities inside a marine reserve in the Caribbean was prevented by the presence of large herbivores that were invulnerable to predation (Mumby et al. 2006). Baskett (2006) used a simple trophic model to evaluate the conditions under which size refugia would prevent

trophic cascades in marine reserves. She found that in general, trophic cascades did not occur when harvest pressure prior to reserve establishment was greater than predation pressure after reserves were enacted, and the presence of size refuges made this outcome more likely. Thus, in cases where prey achieve a size refuge from predation, community change following a management action, such as the implementation of marine reserves, may be significantly delayed until large invulnerable prey are removed by non-predation related causes, such as disturbance, disease, or senescence.

The effect of fisheries on predator size distributions and therefore its consequences on prey dynamics will interact with any geographic variation in predator demography. For example, for the same minimum size limit, a larger fraction of a population with a larger maximum size will be vulnerable to fishing. As a result, an unfished population with a small predator body size distribution may exert less top-down control on the prey population, but in turn may be less affected by fishing. In this study, we examine the interaction of geographic variation in predator demography and size-selective fishing of the predator on predator size distributions. We then examine how variation in predator body size distributions affects the likelihood of size escapes in situations where predators begin eating herbivorous sea urchins at some threshold size and thereafter consume increasingly larger urchins as they themselves grow.

Size-dependent predation on urchins

The release of predation on sea urchins has led to wide-scale conversion of macroalgal communities to urchin barrens devoid of the associated diversity supported by macroalgal habitats (Graham 2004, Ling et al. 2015). Predation on sea urchins in many

ecosystems is size-dependent (rocky reefs in the Mediterranean (Sala 1997); coral reefs in Kenya (McClanahan and Muthiga 1989); and kelp forests in New Zealand (Shears and Babcock 2002, Pederson and Johnson 2006), Tasmania (Ling et al. 2009), and California (Tegner and Dayton 1981)). In Tasmania, the truncation of the size structure of lobsters by intensive fishing resulted in a dramatic reduction in the abundance of large lobsters capable of preying upon adult size classes of a sea urchin that had recently invaded Tasmanian kelp forests due to warming water temperatures (Ling et al. 2009). As a result, in some fished areas where large lobsters were absent, this urchin was able to overgraze kelp forests and create urchin barrens. Case studies such as these have lent support to calls to maintain and restore predator size structure. However, the truncation in size structure was accompanied by a dramatic reduction in total lobster biomass to 2-8% of unfished biomass (Ling et al. 2009). Where both predator abundance and body size are reduced by fishing simultaneously, it is difficult to empirically disentangle the relative role of each. Modeling approaches are particularly useful in this context, by allowing the two effects to be separated.

In this paper, we use a simulation model to evaluate the relative role of predator size distributions and abundance on the top-down control of sea urchin (*Strongylocentrotus* spp.) populations by California sheephead (*Semicossyphus pulcher*) in southern California kelp forests. Like other labrids (Wainwright 1987, 1988, 1991), sheephead display ontogenetic shifts in diet with size: sheephead above 200 mm SL begin eating urchins (Hamilton et al. 2011a, Hamilton and Caselle 2015; Fig. 1A), and thereafter the proportion of the diet comprised of urchins increases. The maximum size of urchins consumed also increases with sheephead size (Hamilton and Caselle 2015), and

larger sheephead preferentially target large urchins (Chapter 2; Fig. 1B). We parameterize the model using this empirical information on size-specific predation on urchins and compare patterns in urchin consumption and resulting urchin population structure given variation in sheephead size distributions and densities. We then test the model with predation rates measured in the field where sheephead size distributions vary.

B. Methods

1. Overview

Sheephead display striking variation in demography and life history over small spatial scales across their range (Hamilton et al. 2011b, Caselle et al. 2011). In general, sheephead grow to larger maximum sizes in the cooler waters of the northern Channel Islands than in the warmer waters further south (569 mm Standard Length [SL] vs. 381 mm; Hamilton et al. 2011). This variation in demographic rates may result in differences in sheephead size distributions, even in the absence of fishing.

To evaluate the relative importance of sheephead size structure and abundance on the capacity for top-down control of urchin populations, we first simulated urchin consumption rates and equilibrium urchin abundance and size structure under scenarios with different sheephead size distributions but (1) equal numbers or (2) equal biomass, in an unfished state. We then tested for the effects of fishing on the predator-prey interaction between sheephead and urchins by using the current minimum size limit of 30cm TL (243mm SL) and the fishing mortality rates of 0.11 estimated by the most recent stock assessement as the ratio of total catch in both recreational and commercial fisheries to total biomass (Alonzo et al. 2004).

To do this, we estimated spatial variation in demographic parameters from populations of sheephead in northern and southern zones of the Southern California Bight using data in Hamilton and Caselle (2015). We simulated sheephead population dynamics and urchin consumption using an age- and size-structured sheephead population model. Equilibrium urchin abundance was then projected with an urchin population model. Modeling details are described in the following sections.

We compared the results to field estimates of mortality as a function of urchin size inside and outside of reserves on Santa Cruz Island, representative of the northern zone with a large asymptotic size, and Catalina Island, representative of the southern zone with a small asymptotic size, but higher sheephead densities and total biomass.

2. Estimating spatial variation in demographic parameters

We estimated location-specific demographic information for the northern (Santa Rosa, Santa Cruz, Anacapa, Santa Barbara, San Nicolas) and southern (Santa Catalina, San Clemente, Palos Verdes, Point Loma) populations of sheephead in the southern California bight from data from 2007-2008 in Hamilton and Caselle (2015) (Table S1). We will hereafter refer to the northern population as "Large Maximum Size" to refer to its larger asymptotic size, while the southern population will be referred to as "Small Maximum Size".

Length at age (SL; mm) is assumed to follow the von Bertalanffy growth function:

$$L_A = L_\infty(1 - exp(-k_{VB}(A - A_0)), \quad (1)$$

where L_∞ is the asymptotic size, k_{VB} is the growth coefficient, and A_0 is the theoretical age at a length of zero. The von Bertlanffy growth coefficient represents the velocity with which fish reach the asymptotic length (van Walraven et al. 2010). A_0 was fixed at zero in order to estimate L_∞ and k_{VB} following Hamilton et al. (2011b) by minimizing the residual sum of squares between the predicted and observed values using the optim function in the stats package of base R.

3. Sheephead Population Model

A deterministic age- and size-structured population dynamics model was constructed to examine the consequences of variation in sheephead size structure and abundance on urchin predation with and without sheephead exploitation. The model is based on that in Hamilton et al. (2011b). Details of the sheephead population dynamics model formulation are in the Appendix.

4. Urchin Consumption by Simulated Sheephead Populations

We used the abundance and size distribution generated by the sheephead population model to simulate urchin consumption in the absence of fishing for (1) the large maximum size population with an unfished recruitment density (R_0) of 100, (2) the small maximum size population with equal R_0 and therefore equal numbers of sheephead as the large population, and (3) the small maximum size population with $2.35R_0$ in order to achieve the same biomass as the large maximum size population. We also examined the effect of fishing on urchin consumption given the current size limit of 243 mm and the current estimated fishing mortality rate (F) = 0.11 from Alonzo et al. (2004).

Daily food consumption (C_A) as a function of sheephead individual body mass (g) was defined from the linear relationship between gut volume (mL) and body mass using the dataset from Hamilton and Caselle (2015) (Fig S1). This represents a maximum daily ration, and may be an overestimate of the absolute value for average prey consumption per day. We use a comparative approach in this analysis, and the relative consumption values are therefore most important to the results rather than their absolute value. Nevertheless, the findings in Cowen (1983) that sheephead stomachs were consistently empty within 1.5 hours of sunrise, and thereafter were relatively full, indicate sheephead frequently consume their full gut volume per day. Prey weight consumed (g) was set equal to gut volume assuming a prey tissue density similar to that of water.

Yearly urchin consumption on size class *i* by the sheephead population was calculated as

$$U_i = 365 \sum_A^{\omega} N_A C_A \theta_{L_A,i} \quad (3)$$

where $\theta_{L_A,i}$ is the percentage of the daily diet of a sheephead of length *L* comprised of urchin *i*.

$$\theta_{L_A,i} = \pi_L \rho_{L,i}, \quad (4)$$

where π_L is the fraction of the gut volume comprised of urchins for a sheephead of length *L*, and $\rho_{L,i}$ is the fraction of total urchins consumed by sheephead of length *L* on each urchin size class *i*. Urchin size classes were set as small (20-35mm test diameter [TD]), medium (35-50mm TD) and large (50-70mm TD). Mean π_L was estimated using a linear model on the proportion of total gut volume comprised of urchins as a function of sheephead size in gut observations from Hamilton and Caselle (2015; Figure 1A). Mean $\rho_{L,i}$ was estimated from field observations of size-specific sheephead predation on

urchins at Catalina Island in 2010 (Chapter 2; Figure 1B-D) by fitting a log-linear multinomial model.

To estimate variation in our estimates of consumption in each urchin size class, we simulated diet data as a function of sheephead size from the moments of the fitted models described in the previous section (Carsey and Harden 2014). The percentage of urchins in the diet for sheephead of a given size was simulated from a normal distribution with a mean equal to the mean percentage of urchins in the diet for each sheephead size, and a standard deviation equal to the residual error of the linear model. Selection of urchin size class by individuals of a given sheephead size was simulated from the mean probabilities of a sheephead of a given size choosing a particular size class predicted from the multinomial model.

5. Empirical Test of the Model

We evaluated the performance of the model by examining empirical mortality rates inside and outside of the Scorpion State Marine Reserve on Santa Cruz Island, representative of Zone 1, and the Catalina Marine Science Center Reserve, representative of Zone 2. To evaluate the concordance of the simulated size distributions to that observed in the field, sheephead populations were surveyed using SCUBA on 60 m^2 belt transects at multiple levels in the water columns (benthic, midwater, and kelp canopy). Transects are laid out in a stratified random design with multiple non-permanent transects in fixed strata relative to the reef edges. At each level in the water a column, a single diver counts and sizes all fish to the nearest centimeter (TL). Santa Cruz was surveyed in 2009-2014 by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO),

and Catalina was surveyed in 2010 and 2011. Sheephead are typically associated with the benthos. As such, only benthic transects in which sheephead were counted within 2 meters of the substrate were included in the analysis. Total length (mm) was converted to standard length (mm) using the equation for $SL = 3.219 + 0.80TL$. Counts of sheephead were binned into 50 mm SL size bins. Biomass in each sheephead size bin was calculated as the product of the number of sheephead in the bin, and the weight-at-length estimated using the length-weight relationship ($W = aL^b$, $a = 3.96 * 10^{-5}$, and $b = 2.944$).

Empirical mortality rates of purple sea urchins inside and outside of reserves at the two islands were estimated using field predation trials. At Santa Cruz Island, ten trials were conducted inside the Scorpion State Marine Reserve (34°03.257′N, 119°34.012′W) and four trials were conducted outside the reserve in July-September 2012 and 2013. At Catalina Island, three trials were conducted at each of three sites inside and outside of the Catalina Marine Science Center reserve (33° 26.817′N, 118° 29.1′W) in August 2011. Five purple urchins of each of three size classes (S: 20-35mm, M: 35-50mm, and L: 50-70mm) were collected from each site. Urchin tests were punctured through the oral and aboral surface using a hypodermic needle. A 20 cm length of monofilament fishing line was threaded through the opening, and used to tether the urchin to a 2-meter length of galvanized steel chain. This technique has been used extensively to assess relative predation rates on sea urchins in reef systems in Kenya (McClanahan and Muthiga 1989), New Zealand (Shears and Babcock 2002), and the Mediterranean (Sala and Zabala 1996, Boada et al. 2015). At Catalina, size-specific mortality of urchins was assessed after 30 minutes. At Santa Cruz Island, mortality was recorded daily for 3 days due to the lower mortality rates observed relative to Catalina.

6. Urchin Population Model

An age-structured urchin population matrix model was developed to examine the consequences of differences in size-specific urchin mortality on urchin abundance and size structure. The population with *n* age classes was projected through time according to the following:

$$\mathbf{N}_{t+1}=\mathbf{A}\mathbf{N}_t + \mathbf{R}, \tag{5}$$

where $\mathbf{N}_t$ is a *n* x 1 vector of abundance in each age class *a* at time *t*, $N_{a,t}$. **A** is a *n* x *n* matrix describing survivorship in each age class:

$$\mathbf{A}=\begin{bmatrix} 0 & & & & \\ S_{1,t} & & & & \\ & S_{2,t} & & & \\ & & \ddots & & \\ & & & S_{n-1,t} & S_{n,t} \end{bmatrix}, \tag{6}$$

where $S_{a,t}$ is the survival at age. **R** is an *n* x 1 vector with the density of new recruits, *R,* in the first entry and zeros elsewhere.

Survivorship in each age class is based on predation mortality at age, M_a, and is reduced further by density dependence:

$$S_{a,t} = (1 - M_a)\frac{1}{1+(\sum_a^n N_{a,t})/\beta} \tag{7}$$

Predation mortality in each size class was assumed proportional to the consumption of urchins by each equilibrium sheephead population simulated above, and constant through time. Predation mortality at age M_a was based on the size at age following the von Bertalanffy growth curve in equation (1) with parameters for purple urchins (L_∞ = 63 mm, k_{VB} = 0.2, A_0 = 0) (Kenner 1992). Survivorship was further reduced due to density dependence according to the second term in equation (7), where β is the carrying

capacity of the population. The minimum age in the model was set to the age at which urchins reached the lower bound of the small urchin size class.

Recruitment of the urchin populations was assumed to be open and equal across scenarios, and R was set equal to 21 recruits per 24 m^2, the median recruitment for urchins in the northern Channel Islands (data from Artificial Recruitment Modules collected by the Kelp Forest Monitoring program, *unpublished*). The carrying capacity, β, was set to 2000 per 24 m^2, to represent minimal density dependence, because urchins can survive at high densities in urchin barrens for many years. An index of equilibrium abundance was calculated as the abundance per m^2 in each urchin size class after 200 years and compared across sheephead populations. Urchin growth rates were varied from the base rate of $k_{VB} = 0.2$ to a slower rate of 0.1, and a faster rate of 0.326.

C. Results

1. Variation in Sheephead Population Structure Due to Demography and Fishing

In the smaller maximum size population, no fish were larger than 400 mm SL (Fig. 2). The size distribution was significantly skewed toward smaller individuals ($D=0.2869$, $p<0.001$), and mean size was 70mm smaller ($t=19.865$, $p<0.001$). Despite equal sheephead numbers in an unfished state, biomass was 2.35 times higher for the population with the larger asymptotic size. As a result, recruitment density needed to be 2.35 times higher in order to achieve the same sheephead biomass.

Because fishing occurs at younger ages (age 5 vs. 8), at a smaller fraction of the maximum length (48% of L_∞ relative to 72% of L_∞), and prior to the size at full maturity (Fig. S2), fishing at the same intensity causes a greater reduction in sheephead biomass

and truncation in size structure when sheephead grow to a large maximum size. Total sheephead biomass was reduced to 59% of unfished levels, compared to 75% of unfished levels with the smaller maximum size (Fig. 2). Mean size was reduced from 263 to 231 mm compared to 196 to 182 mm with the smaller maximum size.

2. Urchin Dynamics with Unfished but Equal Sheephead Numbers

With sheephead numbers equal to the population with large maximum size but a truncated size distribution toward smaller sizes, total urchin consumption was lower overall (23% of that of the population with large asymptotic size; Fig. 3). Patterns of size-specific predation were also reversed, with the population with large sheephead preferentially consuming large urchins, while the population with small sheephead had the highest consumption on small urchins; thereafter consumption declined with urchin size. As a result, consumption of the largest urchins in the small maximum sheephead size population was only 9% of the level consumed by the population with large maximum size (Fig. 3).

The reduction in urchin consumption in the absence of large sheephead led to nearly a doubling in total urchin equilibrium abundance, and a release of the largest urchins, resulting in an approximately 20x increase in the abundance of the largest size class (Fig. 4), and a skewed size distribution towards large urchins.

3. Urchin Dynamics with Unfished but Equal Sheephead Biomass

When equal sheephead biomass was achieved by increasing sheephead recruit density by 2.35 times in the population with small maximum sheephead size, total urchin

consumption was more than double that of the scenario with small maximum size but equal numbers, reaching 54% of the level found with the sheephead distribution with large maximum size (Fig. 3). Consumption of small urchins was more than double that of the scenario with large maximum size, while consumption of the larger size classes was lower (52% and 20% for medium and large urchins, respectively). Despite an 80% reduction in consumption of the large urchins and a lower total consumption rate for the sheephead population with small maximum size, total urchin abundance was actually slightly lower, as was abundance in the small and medium size classes (Fig. 4). The higher mortality on the small urchins served as a bottleneck preventing a size escape: no demonstrable release in large urchins was observed, and size distributions were still dominated by small individuals.

The degree to which predation by the two sheephead populations led to similar outcomes in urchin abundance depended on urchin growth rate (Fig. 5). Where urchins grew slowly through the small size classes, high mortality on small urchins served as an even stronger bottleneck, and urchin abundance was 25% lower for the population with small maximum sheephead size. In contrast, where urchins grew quickly through size classes targeted by smaller sheephead, the bottleneck was weaker, and total urchin abundance was higher (Fig. 5).

4. Effect of Current Fishing (F = 0.11) on Urchin Dynamics

As a result of the greater reduction in sheephead biomass due to fishing the population with larger asymptotic size, total urchin consumption declined by 54%, with the majority of the loss in consumption due to the reduction in consumption of the largest

urchins. In contrast, total urchin predation was reduced by only 42% when fishing either population that grows to a smaller maximum size. Despite a smaller relative decline in urchin consumption due to fishing for the two populations with small maximum size, the effect of fishing on urchin abundance was greater: the proportional increase in total equilibrium urchin abundance after fishing the sheephead with smaller maximum size was slightly higher than the scenario with large sheephead maximum size and equal unfished biomass, and absolute urchin numbers were higher.

5. Empirical tests of model output

Consistent with the results of the simulated populations, mean sheephead size on surveys was smaller at Catalina than at Santa Cruz Island ($t = -6.975$, $p < 0.001$; Fig. 6). Sheephead size was also smaller in fished areas relative to inside the reserve: mean sheephead size was 48 mm smaller outside the reserve at Santa Cruz ($t = -3.278$, $p=0.001$) and 36 mm smaller on Catalina Island ($t = -2.625$, $p =0.009$; Fig. 6). Because sheephead density was higher, total biomass was greater at Catalina in the reserve despite the lack of large sheephead, and biomass was equal between the Catalina fished areas and the Santa Cruz reserve. This higher density at Catalina may be fueled by higher recruitment: mean recruit density is 6 times higher at Catalina Island (Fig. S3).
Urchin mortality rates were higher inside the reserve at Catalina for all urchin size classes ($F_{1,51}=22.3$, $p <0.001$), with no significant effect of urchin size on mortality ($F_{2,51}=1.98$, $p=0.15$), likely driven by the consistently high mortality rates across size classes in the reserve. Outside the reserve, mortality was much lower on the large urchin size classes, consistent with the results of the simulation model for the southern zone. In contrast, the

effect of reserve protection at Santa Cruz differed with urchin size ($F_{2,36}$=4.2803, p=0.02), with higher mortality rates on the largest urchins in reserve, but comparable levels for smaller urchins. This qualitatively matches the results from the simulation model for the northern zone.

D. Discussion

Given ontogenetic shifts in diet composition, predation rates on prey eaten late in the life of the consumer are severely reduced when the size distribution of predators was truncated toward small sizes, either due to removal by size-selective fishing or due to spatial demographic differences in the asymptotic size attained (Chapter 1). Had the prey consumed by large-bodied predators been a different species than that eaten by their smaller-bodied counterparts, the absence of large predators would result in prey release, causing changes in prey population dynamics that could not be counteracted by the addition of higher numbers or biomass of small-bodied predators. However, when ontogenetic shifts in predator diet involved increasing consumption of larger sized prey of the same species, as was the case for the urchin case study presented here, the ecosystem consequences of truncation in predator size distributions depended on how predator biomass was affected. When predator biomass was maintained, truncated size distributions toward smaller predator sizes did not result in explosions in prey abundance nor size escapes for the largest prey. In this case, the greater abundance of small predators resulted in elevated consumption rates of small prey, and caused a strong bottleneck that limited prey population growth. Despite a dramatic reduction in consumption of large prey (owing to the loss of large bodied predators), no size escape of

the large prey was observed. This result was in stark contrast to the observed prey outbreak (both total numbers and large size prey) that occurred when predator sizes were truncated but equal *numbers* of predators were maintained in the population.

Thus, two alternative pathways can prevent build-up of prey in large prey size classes: (1) high mortality on large prey through the consumptive activities of large predators, and (2) high mortality on small prey, which prevents sufficient numbers of individuals from surviving to large sizes. As a result, this study challenges some of the basis for size-based indicators that monitor changes in predator size distributions alone. One such indicator, the Large Fish Indicator is currently in use in the North Sea (Greenstreet et al. 2010). This indicator monitors the fraction of the total fish community biomass on trawl surveys comprised of fish larger than 30 cm as a measure of "ecological quality", with a target of 30%(Greenstreet et al. 2010). The results of this study suggest that where small predators eat the same prey species as large predators, but target smaller size classes, declines in predator size structure may not inherently lead to lower ecological quality if predator biomass is maintained. The fact that no urchin barrens currently exist either in the marine reserves or the fished areas we studied on Catalina Island (*pers. obs)* lend support to the conclusion that high sheephead biomass and the observed high relative mortality rates on small urchins can counteract the relative absence of large sheephead and contribute to kelp forest resilience. However, it is important to note that where fisheries, and not the environment, drive truncation in sheephead size structure, it is unlikely that predator biomass will be maintained, and fishing may compromise this resilience.

As a result of spatial variation in sheephead demography, size-selective fishing had a larger effect on the biomass and mean size of the population where sheephead attained larger maximum sizes. In conjunction, urchin consumption declined by a greater extent from the unfished to the fished state. However, in contrast to our expectations, the relative effect of fishing on equilibrium urchin abundance was greater for the population with smaller maximum size. This was likely due to the fact that mortality on the small urchins was reduced to a greater extent by fishing the sheephead population with small maximum size, and variation in mortality in this size class had the biggest effect on overall urchin abundance.

For California Sheephead, maximum sizes are inversely related to population densities (Cowen et al. 1991; Caselle et al. 2011), and dwarf populations may result (Warner 1975). Stunted individual growth in the southern zone may result from the 6-fold higher recruit densities (Fig. S3). Diets of sheephead at Catalina island are dominated by prey items of poorer quality relative to individuals collected in the northern Channel Islands (Hamilton et al. 2011a), suggesting strong intra-specific competition for resources may be limiting growth, or environmental conditions are limiting prey availability and quality. Alternatively, the differences in water temperature observed between the zones may also be contributing to the observed differences in size at age. Although the mechanisms remain poorly understood (Angilletta 2004), ectotherms like fish are thought to achieve larger body sizes in colder water temperatures, based on observations of larger individuals at higher latitudes in natural environments (Fisher et al. 2010), a phenomenon described as “Bergmann’s rule” and laboratory animals reared under colder temperatures growing to larger body size—“the temperature size rule”

(Angilletta and Dunham 2003). If climate change results in warmer water temperatures in the northern zone, those populations may also respond with smaller size at age that may compromise the capacity for these populations to regulate urchin prey.

On the other hand, a reduction in size at age can be caused not by the environment but by fisheries-induced evolution. By selecting the largest individuals and thereby altering size-dependent mortality, fisheries can impose selection pressure for smaller size at age, and therefore slower growth. In the laboratory, Conover and Munch (2002) demonstrated that selectively harvesting the largest 90% of the population led to declines in growth such that both weight at age and total yield was half that of a population in which the smallest 90% were harvested in just 4 generations. While these selection differentials are more extreme than most fisheries, Brown et al. (2008) found that comparable results would be true over more generations in wild populations using realistic fishing pressures.

Even if fisheries do not directly affect growth, selective fisheries commonly reduce the size at maturation (Dunlop et al. 2009). Investment in reproduction comes at the expense of growth. As a result, fisheries selection for earlier maturation can indirectly lead to reductions in size at age (Enberg et al. 2012) without selecting for slower growth. Where evolution to slower growth or smaller sizes at maturation have occurred, these changes have the potential to be irreversible, even after the cessation of fishing, if sufficient genetic variation no longer exists in the population. Reductions in size at age due to fishing may be contributing to the smaller size distributions of sheephead at Catalina. In the 1970s, growth parameters for Catalina were equivalent to current levels at Santa Cruz Island (Fig. S4, Table S2). To the extent to which smaller size at age at

Catalina is due to fishing-induced evolution rather than a plastic trait due to environmental conditions, the capacity for the population to regulate urchin populations may be sensitive to reductions in sheephead recruitment that would reduce sheephead biomass without concordant increases in sheephead size at age.

The capacity for small predators to create a sufficient bottleneck and maintain top-down control in prey depended on the life history characteristics of the prey. Where prey grow quickly through the size classes vulnerable to small predators, the lack of large predators may still result in an increase in prey abundance and release of large prey, resulting in skews in prey size distributions toward larger individuals. Just as the environment can influence the growth and maximum sizes of predators, more productive environments can also support faster growth in prey and an increased likelihood that they achieve this size refuge (Chase 1999, 2003). As a result, predator effects on prey populations are weaker with high primary productivity when prey can achieve a size refuge (Chase 1999, 2003). Likewise, a long-term nutrient enrichment experiment in a forested stream led to dominance by large-bodied primary consumers that were invulnerable to predation, and a decoupling of primary consumer and predator production (Davis et al. 2010). Nutrient enrichment is common due to human activities, and may affect the capacity for gape-limited predator populations to regulate prey where prey achieve a size refuge. Climate change is also predicted to change productivity (Behrenfeld et al. 2006), which may interact with climate-induced changes in predator size distributions to affect prey abundance, the presence of size refugia, and ecosystem dynamics.

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F. Figures

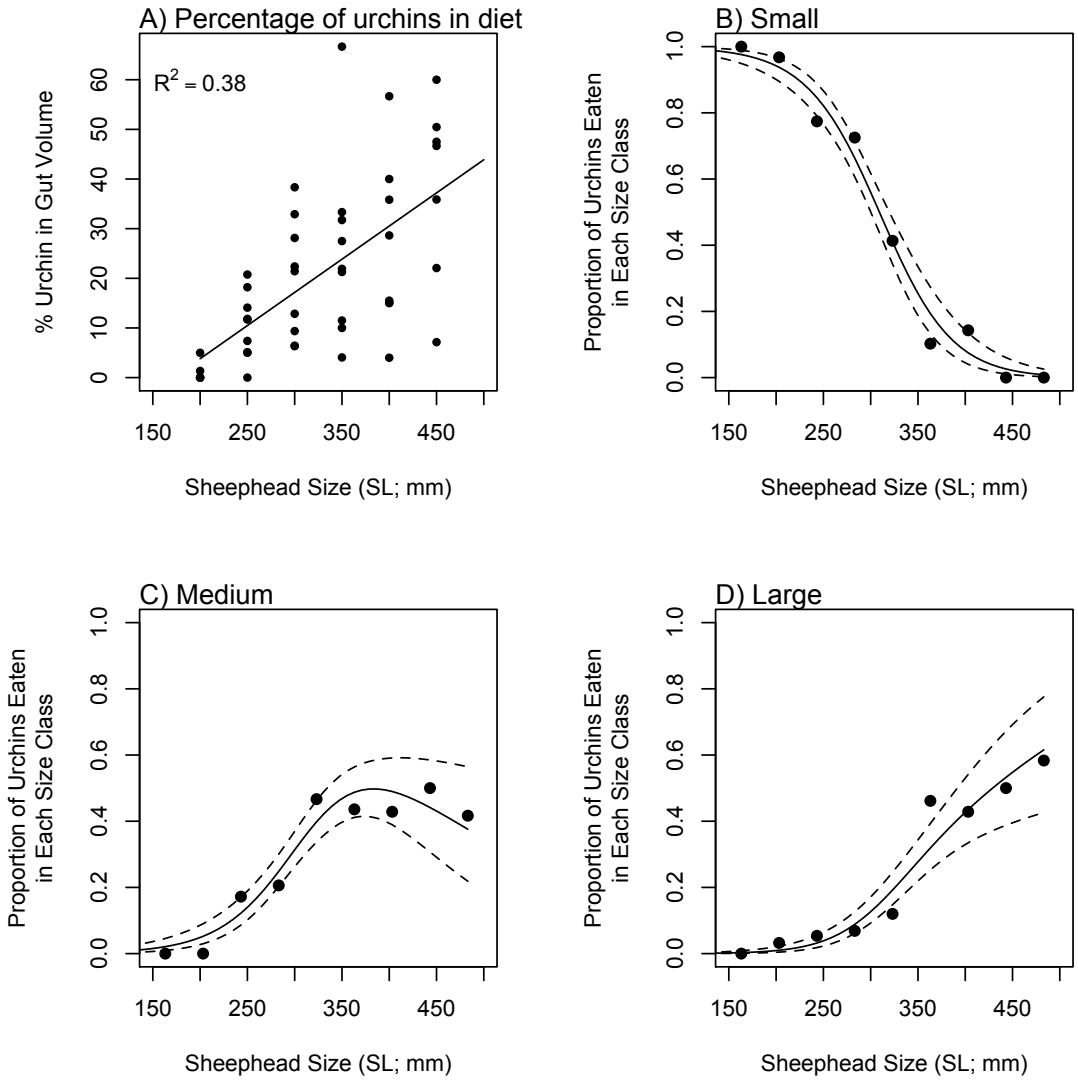

Figure 1. A) Observed (dots) mean percent of urchins in gut as a function of sheephead size (SL (mm)) for 9 locations in southern California. Data from Hamilton and Caselle (2015). Predicted percentage of urchin in diet from linear model (line; R^2=0.38). For every 50mm increase in standard length, the percent of the diet comprised of urchin increased by 6.7%. B-D) Urchins eaten in each urchin size class as a proportion of all urchins eaten by sheephead size (SL; mm) observed during feeding trials at Catalina Island (symbols), and the mean (solid line) and 95% confidence intervals (dashed lines) on the prediction from a multinomial logistic regression. B) Small (20-35mm test diameter (TD)) C) Medium (35-50mm TD): D) Large (50-70mm TD). Data from Chapter 2.

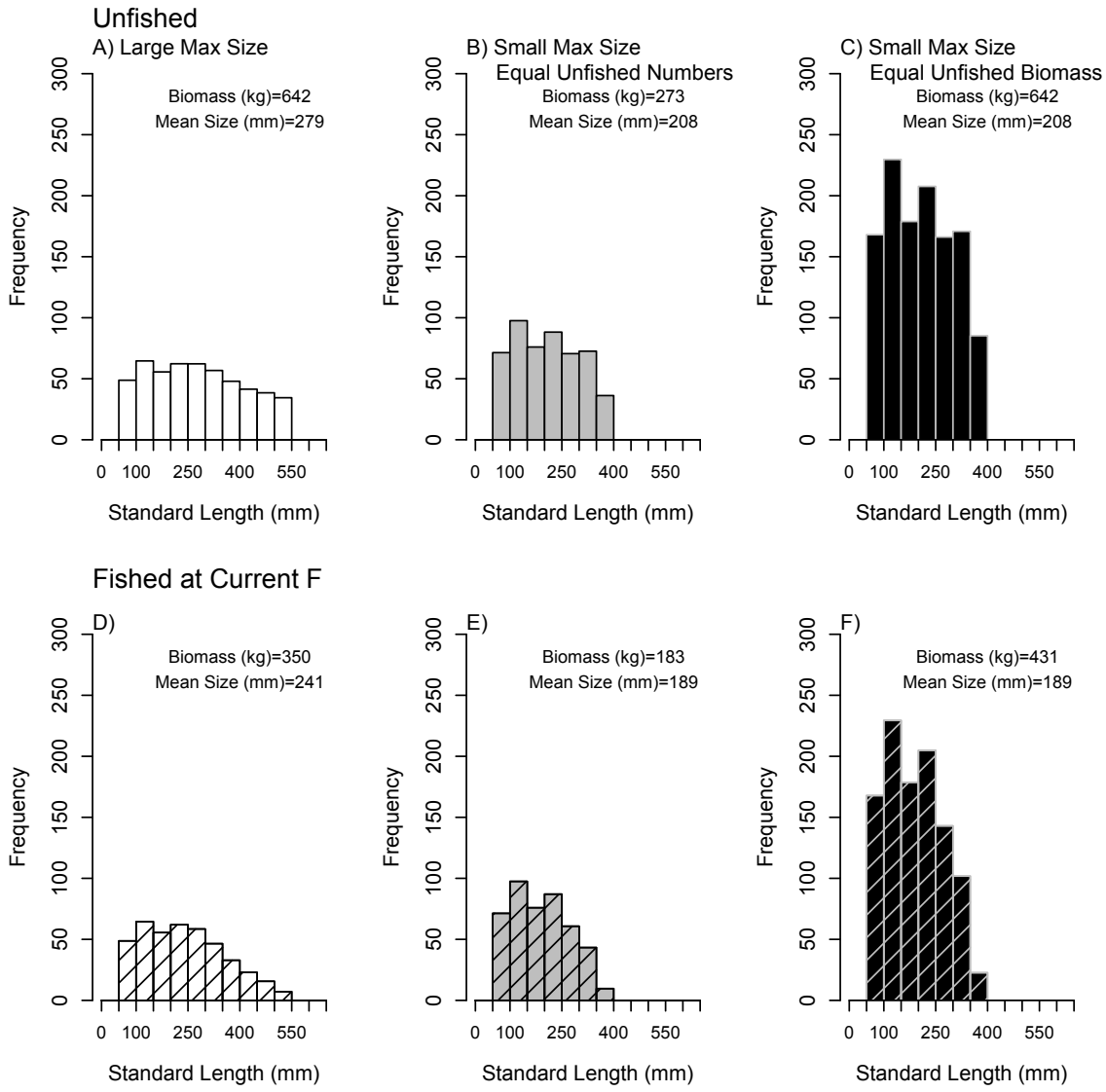

Figure 2. Frequency of California sheephead in each size bin for a simulated unfished (A-C; open bars) population, and for a simulated population fished at the current fishing mortality rate (F=0.11) (D-F; hashed bars) with demography based on large maximum size (A, D; white), small maximum size and equal unfished numbers of predators (B, E; gray), and small maximum size and equal unfished biomass (C, F; black).

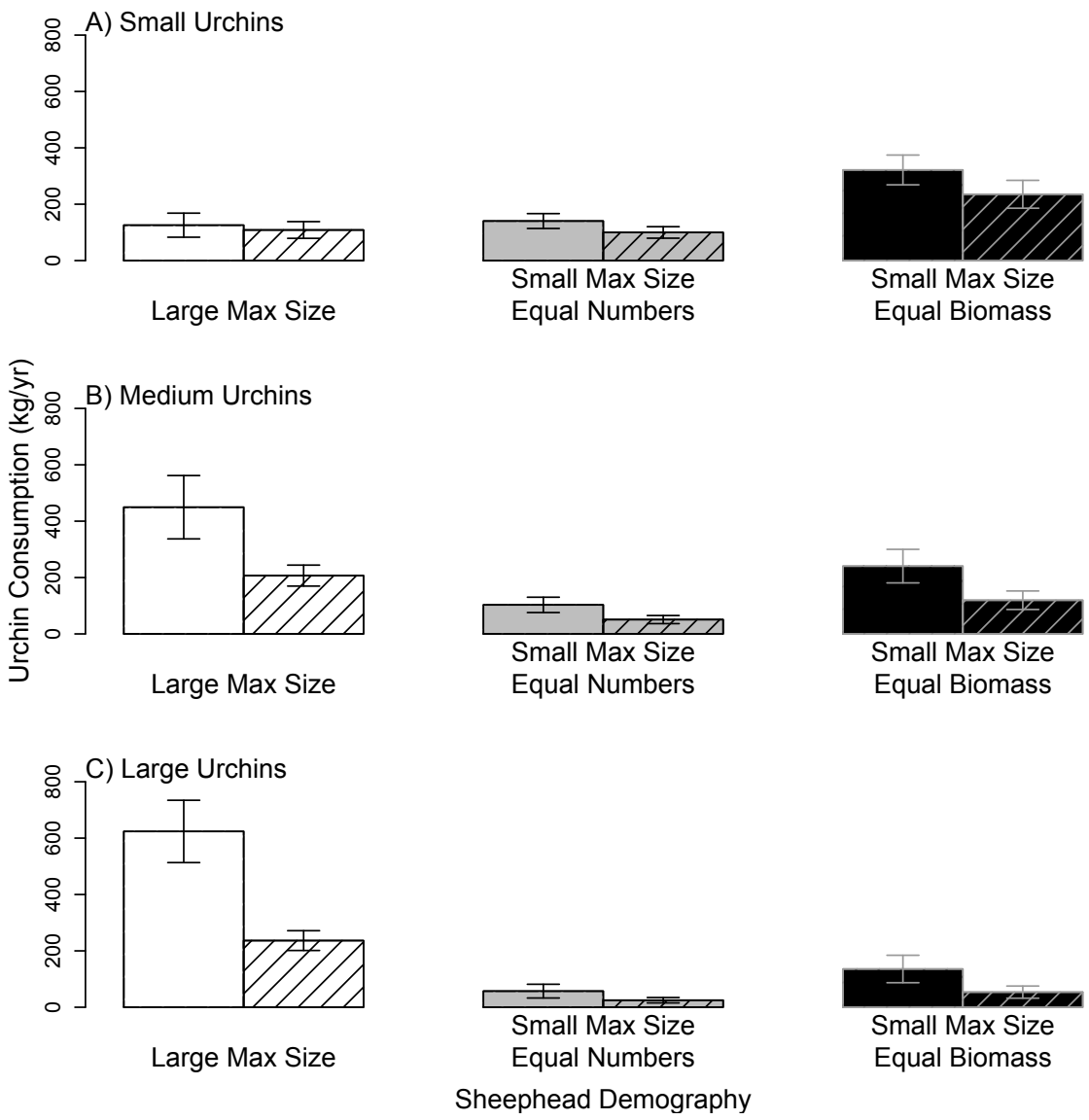

Figure 3. Urchin consumption (kg/yr) by sheephead in each of three urchin size classes (A) small, (B) medium, and (C) large for unfished (open bars), and fished (hashed bars) sheephead populations with demography based on large maximum size (white), small maximum size and equal unfished numbers of predators (gray), and small maximum size and equal unfished predator biomass (black). Error bars represent standard deviation from the mean given variation in predicted total urchin consumption and size preferences.

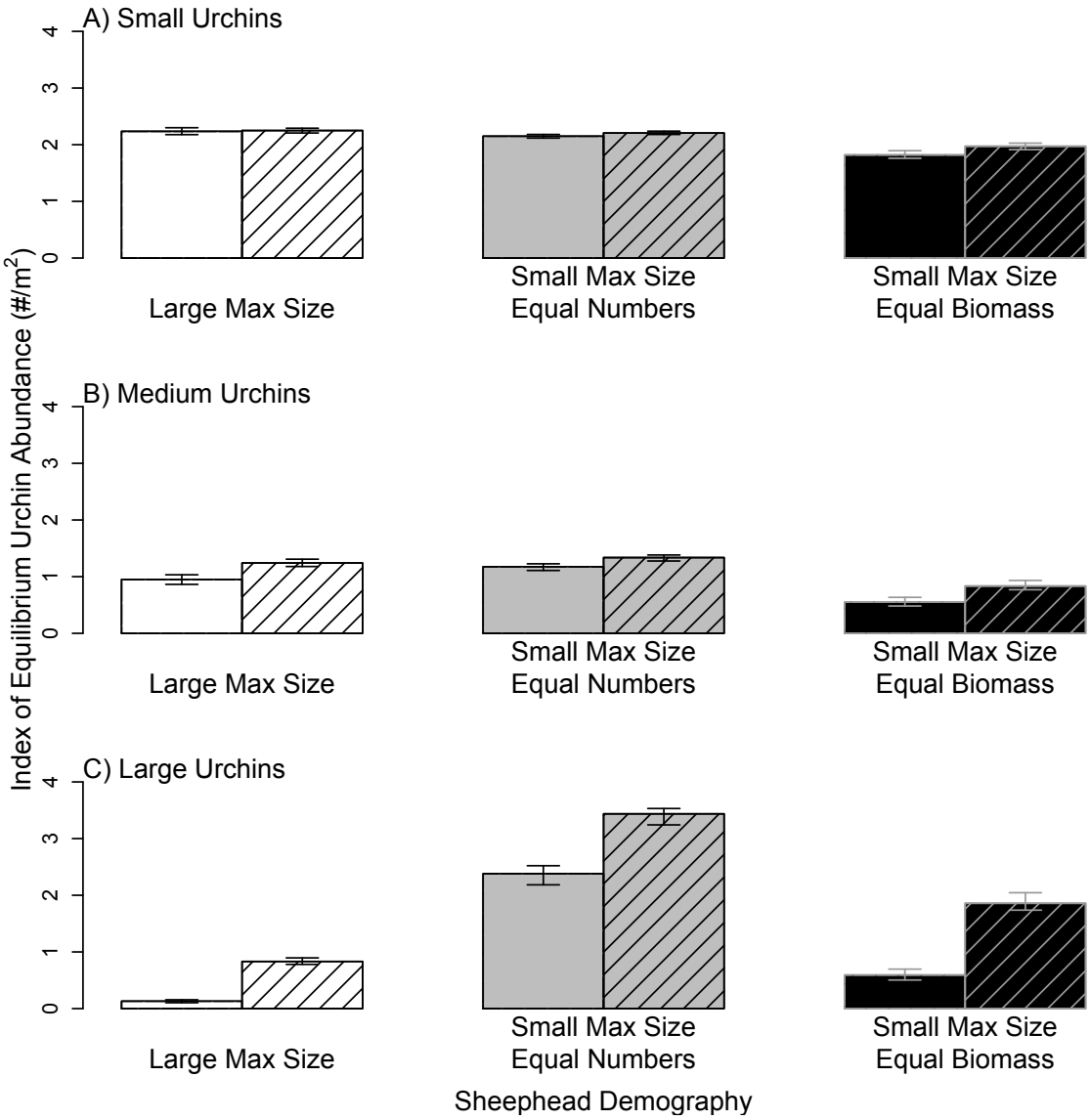

Figure 4. Index of equilibrium urchin abundance (#/m^2) in each of three urchin size classes (A) small, (B) medium, and (C) large for unfished (open bars), and fished (hashed bars) sheephead populations with demography based on large maximum size (white), small maximum size and equal unfished numbers of predators (gray), and small maximum size and equal unfished biomass (black). Bars represent median values, and error bars represent first and third quartiles.

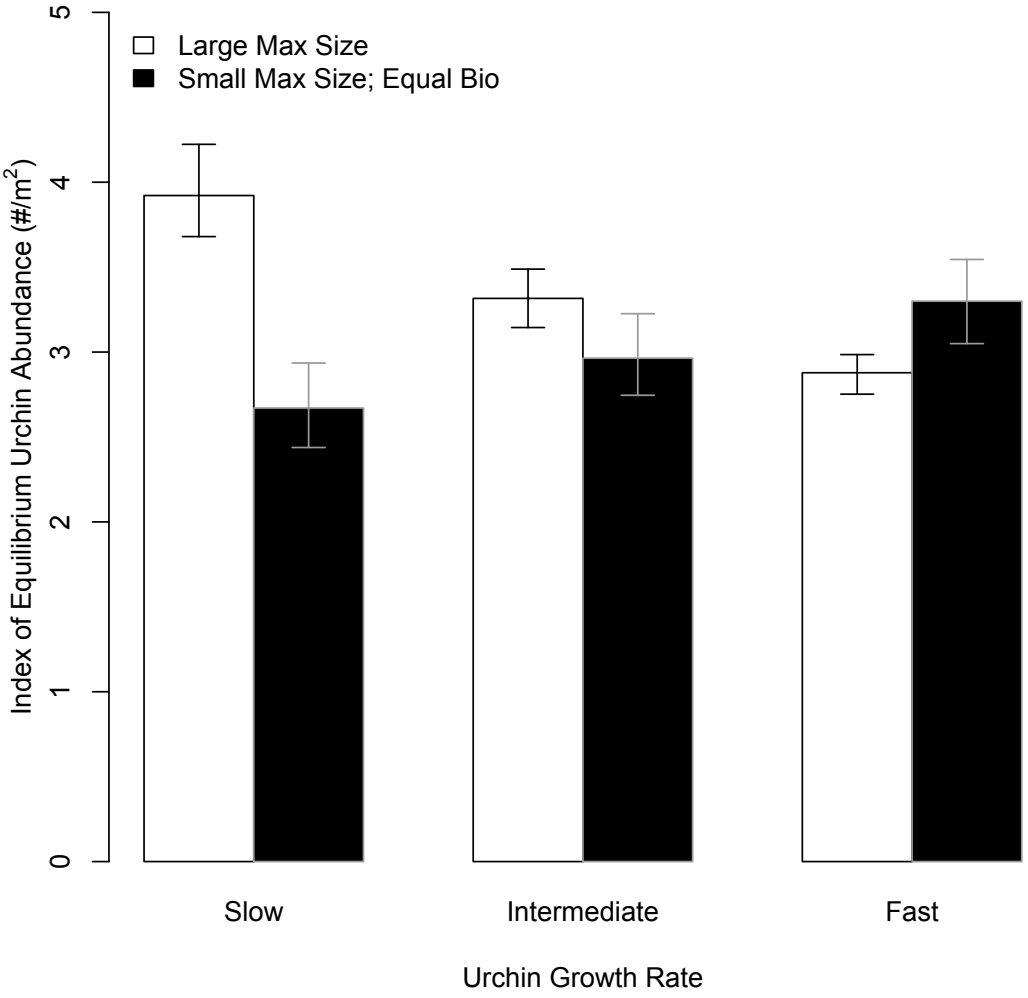

Figure 5. Comparison of total equilibrium urchin abundance (#/m^2) given differences in urchin growth rates when preyed upon by unfished sheephead populations with large and small maximum sizes and equal biomass. Bars represent median values and error bars represent first and third quartiles.

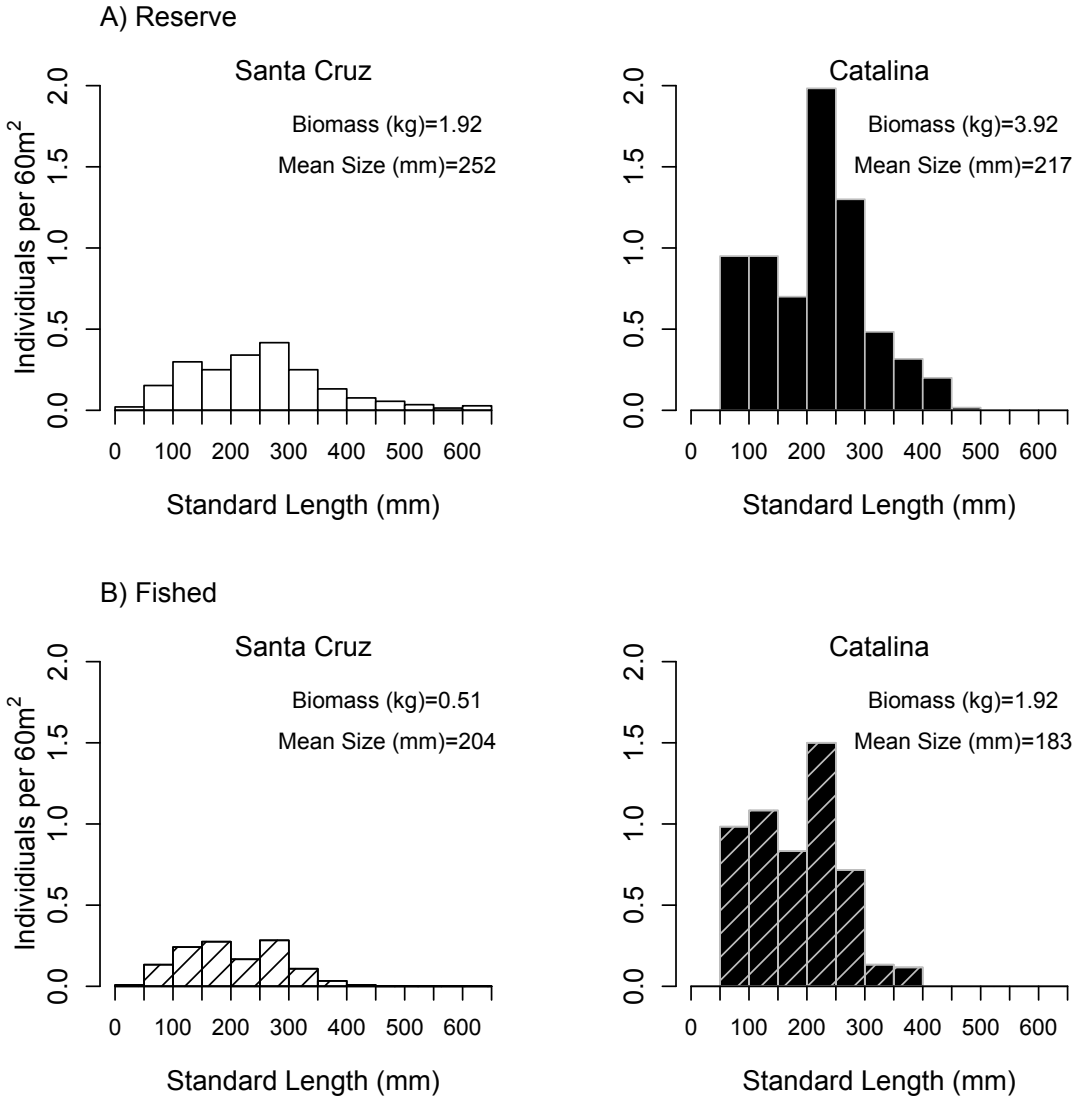

Figure 6. Observed size frequency per transect inside (A) and outside (B) of the Scorpion State Marine Reserve 2009-2014 (N= 298 and 151, respectively) on Santa Cruz Island, and the Catalina Marine Science Center State Marine Reserve in 2010 (N=223 and 181) on Catalina Island, representative of large maximum size and small maximum size demography, respectively.

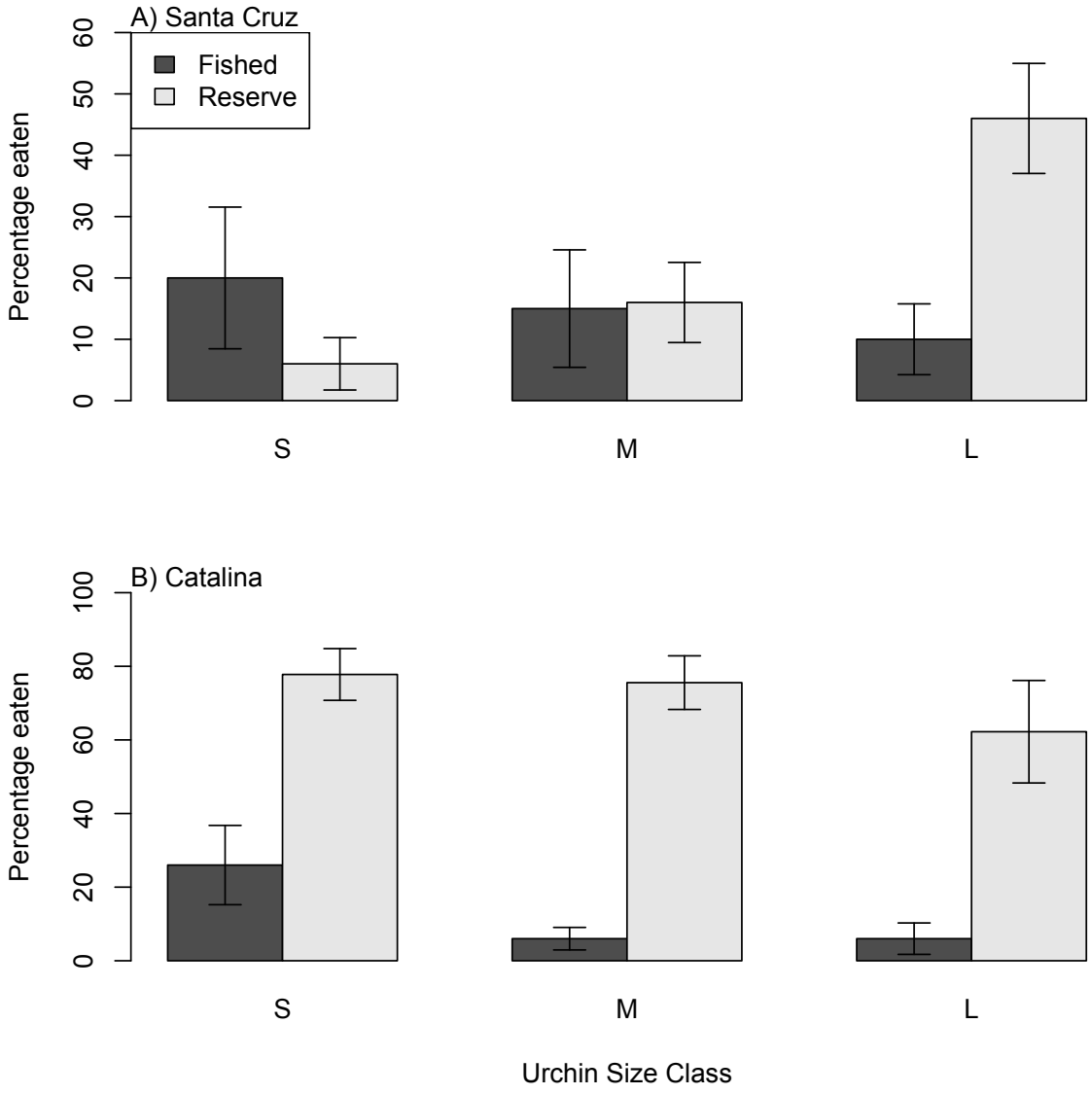

Figure 7. Size-specific mortality rates of purple urchins measured in the field inside and outside of marine reserves at A) Santa Cruz Island and B) Catalina Island. The percentage of urchins eaten was recorded at Santa Cruz after 3 days, and after 30 minutes at Catalina.

G. Appendix

1. Supplementary Methods: Sheephead Population Dynamics Model

The stable age structure for the sheephead population model is given by:

$$N_A = \begin{cases} R_F & A = 0 \\ N_{A-1}\exp\left(-(M + FS_{A-1})\right) & 0 < A < \omega \\ N_{A-1}\exp\left(-(M + FS_{A-1})\right)/[1 - \exp\left(-(M + FS_A)\right)] & A = \omega, \end{cases} \quad \text{(A1)}$$

where N_A is the number of animals of age A, M is the instantaneous rate of natural mortality, F is the fishing mortality when selectivity is equal to 1, and S_A is the selectivity of animals of age A to the fishery. ω is the maximum longevity of 20 years as per Alonzo et al. (2004), representing a "plus group" in which all fish that would have survived to another year are accumulated in this group, and assumed to have an age of 20. R_F is the number of recruits based on a Beverton-Holt stock-recruit relationship when fully selected fishing mortality equals F:

$$R_F = \frac{E_F}{(\alpha + \beta E_F)}, \quad \text{(A2)}$$

where α and β are parameters of the Beverton-Holt spawner-recruit curve and E_F is the egg production by the fished sheephead population such that

$$E_F = \sum_{A=1}^{\omega} N_A f_A \delta_A, \quad \text{(A3)}$$

where f_A is the number of eggs produced by a female of age A, and δ_A is the fraction of mature females in the population. Because California sheephead are sex-changing fish, the fraction of mature females in the population (δ_A) initially increases with maturity, then declines as larger individuals change sex into males. The size at maturation, $L_{50♀}$, was estimated from the fraction of immature females in 20mm length bins in each population, ρ_A:

$$\rho_A = 1 - \frac{1}{1+\exp\left(-k_{♀}\left(L_A - L_{50♀}\right)\right)} \quad \text{(A4)}$$

The size at sex change, $L_{50♂}$, was estimated from the fraction of mature males in 20mm length bins in each population, φ_A:

$$\varphi_A = \frac{1}{1+\exp\left(-k_{♂}\left(L_A - L_{50♂}\right)\right)} \quad \text{(A5)}$$

$$\delta_A = \rho_A - \varphi_A$$

Parameter values were estimated by minimizing the sum of squared residual error of the predicted from the observed data.

The fecundity at age (number of eggs produced) was calculated by using the allometric relationship between sheephead length in mm and the number of oocytes in Loke-Smith et al. (2012):

$$f_a = a_{fec}(L_a)^{b_{fec}} \quad \text{(A6)}$$

where $a_{fec} = 3 \cdot 10^{-9}$, and $b_{fec} = 5.537$. The size-fecundity relationship was assumed to be constant across sites.

The parameters of the Beverton-Holt spawner recruit curve are defined as

$$\alpha = \frac{E_0}{R_0}\left(1 - \frac{h-0.2}{0.8h}\right) \quad \text{(A7)}$$

$$\beta = \frac{h-0.2}{0.8hR_0}$$

where E_0 is egg production in the absence of fishing, R_0 is recruitment in the absence of fishing, h is the steepness of the stock-recruitment relationship (the fraction of R_0 when E is reduced to 20% of the virgin, or unfished E [E_0]. We set steepness equal to 1, to coincide with the value used in the stock synthesis model in the 2004 stock assessment (Alonzo et al. 2004), based on a lack of demonstrable spawner-recruit relationship.

Numbers are converted to biomass using the length-weight relationship where biomass in each age class is the product of N_A and W_A where W_A is the weight of an animal of age A in kg based on the allometric growth model ($W=aL^b$), where a and b were estimated for the pooled population ($a = 3.96 * 10^{-5}$ and b=2.944).

Values for natural mortality (M) were assumed to be equal (0.2) across all populations, as per the stock assessment (Alonzo et al. 2004). Unfished recruitment (R_0) was modeled under a scenario of equal recruitment of 100 individuals to achieve equal numbers of predators in an unfished population, as we all as with 2.35 times the recruitment in Zone 2 in order to achieve equal unfished biomass with the "Small Linf" demography.

The probability of capture by the fishery for an individual of a given age is determined by a minimum size limit and is modeled as the probability that an individual of a given age is greater than the current minimum size limit of 243mm SL given variation in length at age (CV=0.1) as described by a logistic equation.

2. Supplementary Tables

Table S1. Demographic parameters for sheephead populations fitted to demographic information from Hamilton and Caselle (2015). Recruitment was adjusted so that one scenario had equal predator numbers to the large maximum size scenario, and the second scenario had equal predator biomass.

Parameter	Large Maximum Size	Small Maximum Size	
		Equal Numbers	Equal Biomass
L_∞	569	381	381
k_{VB}	0.14	0.18	0.18
$L_{50♀}$	262	206	206
$k_♀$	0.11	0.055	0.055
$L_{50♂}$	409	273	273
$k_♂$	0.052	0.025	0.025
R_0	100	100	235

Table S2. Demographic parameters for Catalina from 2007-2008, the historical population in the 1970s, and at Santa Cruz Island for 2007-2008.

	Catalina 2007-2008[1]	Catalina 1970s[2]	SCI 2007-2008[1]
L_∞	305.3	547	553
k_{VB}	0.245	0.129	0.152
$L_{50♀}$	199	209	260
$k_♀$	0.08	0.113	0.437
$L_{50♂}$	225	317.14	405
$k_♂$	0.075	0.027	0.0822

[1] Data from Hamilton and Caselle (2015)
[2] Data from Warner (1975)

3. Supplementary Figures

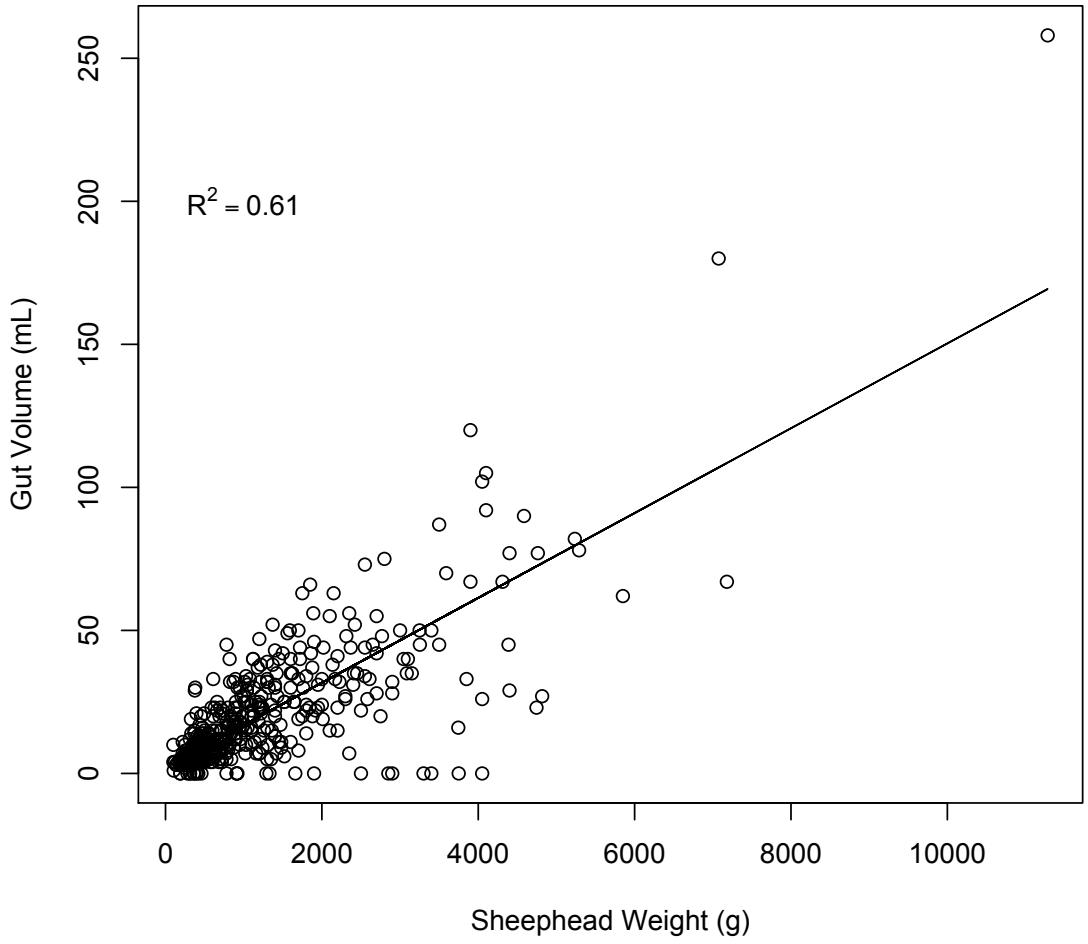

Figure S1. Relationship between gut volume (mL) and sheephead body weight (g) using data from Hamilton and Caselle (2015). The linear model predicted gut volume = 2.072 +0.015 W_A, where W_A is the weight at age in grams.

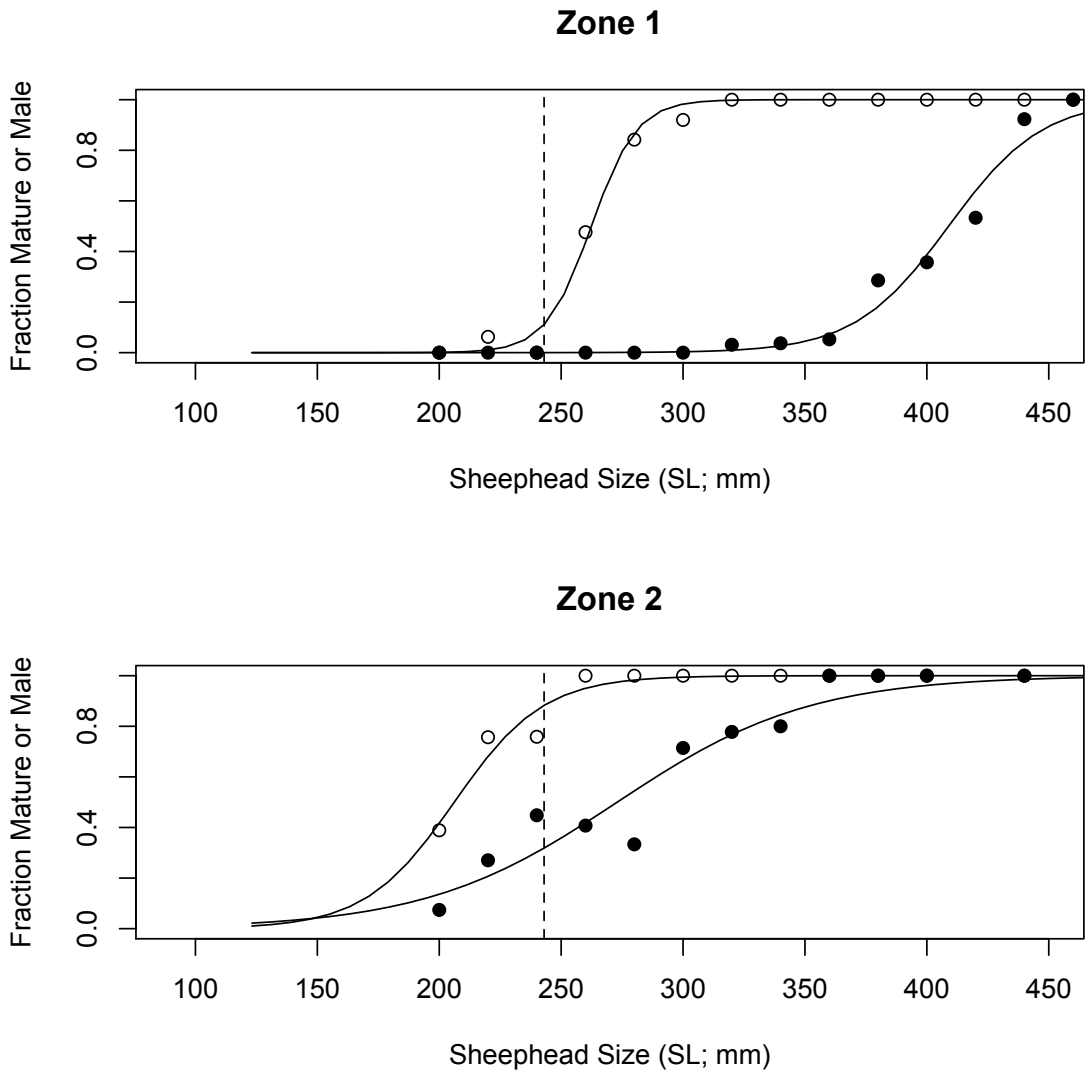

Figure S2. Observed size at maturity (open circles) and sex change (filled circles) in Zone 1 and Zone 2 and that predicted from fitting logistic curves to observed data (solid lines). The dashed line represents the current size limit at 243mm SL.

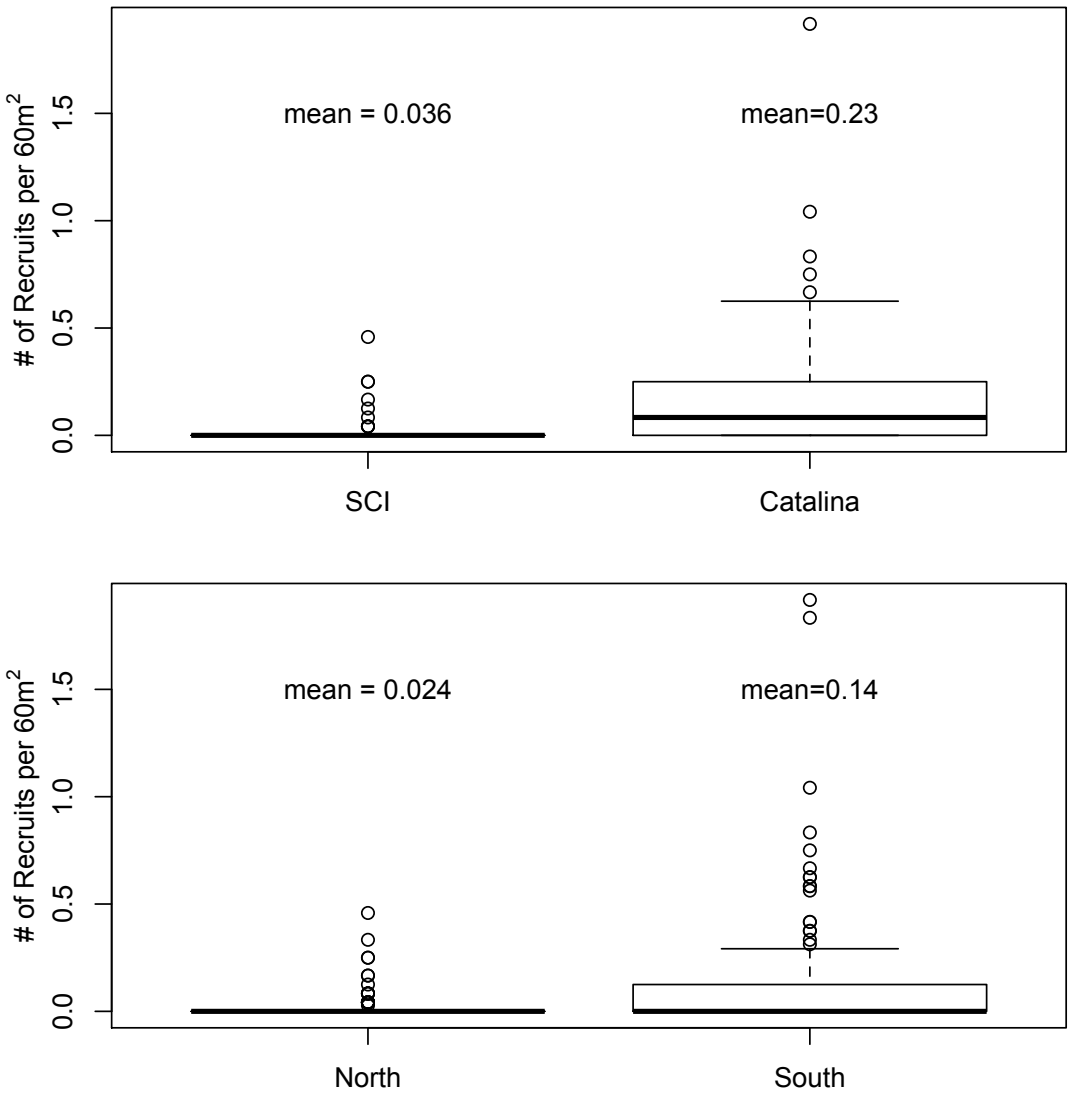

Figure S3. Density of sheephead recruits at Santa Cruz Island and Catalina, and for all islands combined in the northern zone and in the southern zone. Recruit density was estimated from the number of individuals less than 100mm SL using $60m^2$ visual surveys conducted in 2004, 2008, 2011, and 2012 by the Vantuna research group and PISCO. Recruitment is 6 times higher at Catalina, and in the southern zone.

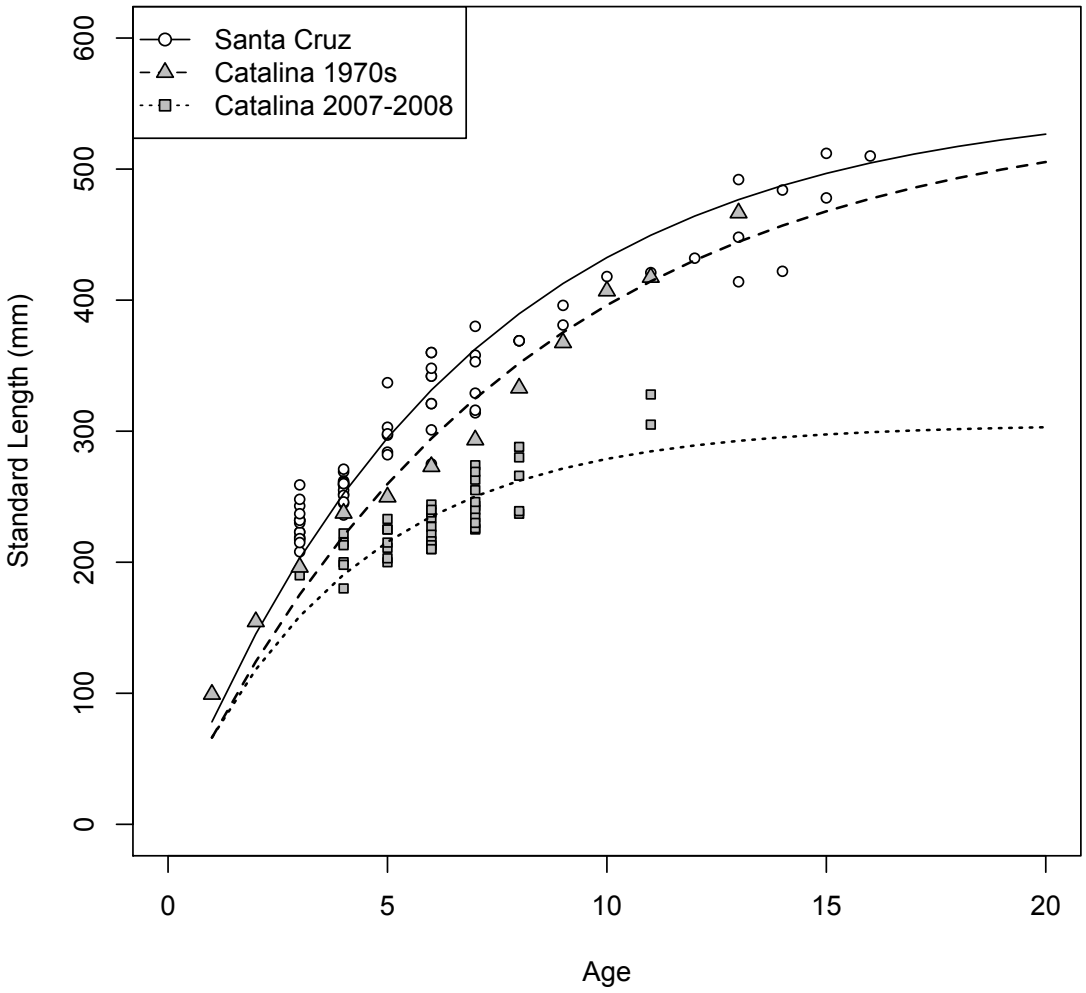

Figure S4. Observed length at age (symbols) and that predicted from fitting von Bertlanffy growth curves (lines) for Santa Cruz Island in 2007-2008 (open circles and solid line; data from Hamilton and Caselle 2015), Catalina in the 1970s (gray triangles and dashed line; data from Warner 1975), and Catalina in 2007-2008 (gray squares and dotted line; data from Hamilton and Caselle 2015)